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ENDEAVOUR

The British quarterly scientific journal ENDEAVOUR was first published, by Imperial Chemical Industries Limited, in January 1942. Its purpose is to provide scientists, especially those overseas, with news of the progress of the sciences. While emphasis is laid upon British work, occasional articles from overseas contributors are included and impartial reference is made to the world's scientific literature. To make the journal truly international in character it is published in five separate editions—English, French, German, Italian, and Spanish.

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The drawing on the cover is of the bark Endeavour, *which, commanded by Captain James Cook and carrying a number of scientific workers, was sent out by the British Admiralty in* 1768 *to chart the South Pacific Ocean and observe the transit of Venus*

ENDEAVOUR

A quarterly review designed to record the progress of the sciences in the service of mankind

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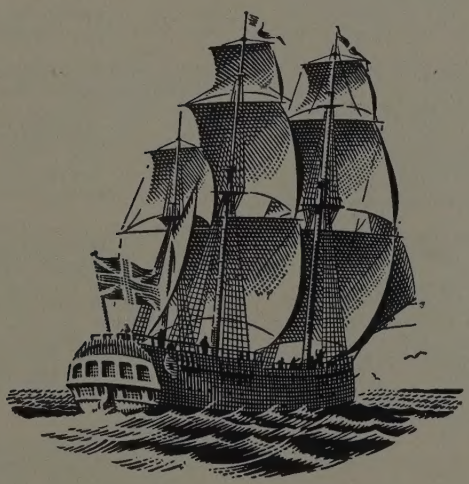

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Organization in research

There are many indications that science is developing so rapidly that it is in danger of being retarded by its own weight unless drastic action is taken. It is, for example, no uncommon experience to find that simply through lack of material resources promising fields revealed by some new discovery can be explored only slowly or not at all. The volume of publication is now so great that for even the comparatively narrow specialist it is often difficult, if not impossible, to find time to read all that usefully pertains to his own subject. With new scientific journals constantly being established, existing ones increasing in size, and the output of books growing daily, it is certain that the problem of utilizing the literature will become even more serious unless there is some systematization of knowledge far in excess of anything hitherto considered. When new knowledge is accumulating faster than it can be mentally assimilated even by those within whose immediate field it lies, it is not surprising that its useful application is still further in arrears, for as a general rule the translation of a useful idea into a workable industrial process is long and laborious, entailing much additional research. There is some truth in the often heard assertion that if all pure research were stopped today, we should still have ample ideas to develop for many years to come.

The question of the ultimate limits of knowledge —what the human brain can grasp and what is beyond its capacity—is one of no immediate practical importance, since any such limits seem to lie well beyond our present boundaries. But in present circumstances, when the whole future of our material civilization is so intimately bound up with science and its useful application, one aspect of this question is of the utmost importance. How, with our limited resources, can the extension of our knowledge by research, both pure and applied, be effectively speeded up?

Here a major factor is clearly lack of scientific manpower, which is causing grave concern. Although urgent steps to increase it are being taken in many countries, there must be a natural limit to the expansion possible, for neither is there unlimited talent available nor is it possible, without far-reaching disturbance of national life, to divert more than a fraction of a country's manpower into scientific and technical channels. If we cannot indefinitely increase our scientific and technical manpower we must take steps to see that those available are more productive. In many sections of industry this proposition has already been accepted and put into practice, although it is only quite recently that the general public has become aware of the process—which promises to deserve the title of industrial revolution—and has begun to express concern about its social and economic consequences.

The Industrial Revolution which began in Britain in the eighteenth century is inappropriately named, for it implies a violent process which in reality never took place. Although profound and far-reaching changes occurred, they took place fairly gradually and without acute social upheaval. Even the advent of mass-production methods on the assembly-line principle—which many saw as the harbingers of mass unemployment—brought no acute difficulties, for it soon became clear that far from reducing the need for labour they in fact stimulated demand for it.

Now, two centuries later, we seem already to be in the first stages of a second industrial revolution, comparable with the first in both its importance and gradualness. As the first led to the elimination of much heavy manual toil in industry, so the second will eliminate much mental drudgery. This process is commonly known as automation, but at present the term is rather loosely applied. Frequently it is taken to imply no more than an intensive mechanization of repetitive industrial operations, in which devices incorporated within the machines themselves automatically compensate for departures from the desired performance. But many regard this kind of automatic mechanization as merely a manifestation of automation, which in its fullest sense is taken to mean the organization of highly complex work in such a way that it can be carried out by relatively unskilled workers.

The process is commonly regarded as being primarily of industrial significance, and there has been comparatively little consideration of how it might assist science. But this child of science seems well adapted to help its parent in its present problems, for these are in many respects comparable with those of modern industry. Both science and industry labour under a common difficulty: they have highly complicated operations to perform but, for both practical and economic reasons, insufficient technical manpower to carry them out by present methods. Both can ease their burden and extend their activities either by assigning

more and more of their routine operations to automatic devices or by breaking their work down into simple steps which can each be undertaken by workers who have had only a little training.

Almost every well equipped laboratory can now furnish examples of the mechanization of complex operations. Such examples as self-recording infrared spectroscopes, automatic balances, chromatographic fraction-cutters, and automatic particle-counters come at once to mind. Devices such as these are, of course, doubly useful. On the one hand they save a great deal of time, and this can be devoted to more original work. On the other, they may make possible the undertaking of projects which although theoretically feasible are by ordinary methods too laborious to be embarked upon at all. For example, much of the recent progress in protein chemistry undoubtedly stems from the fact that paper chromatography has in effect provided, by comparison with the methods previously available, a method of mass-producing accurate and complete analyses of amino acid mixtures. Again, the recent rapid progress in X-ray crystallography—where there have been spectacular determinations of the structures of some very large molecules—has to a considerable extent resulted from the rapid analysis by automatic computing machines of the great quantity of data collected. Although in the important field of extracting information from the vast mass of scientific literature the methods of half a century ago still prevail, some progress towards mechanization has been made, and experiments with electronic translating machines have shown promise.

This kind of procedure seems capable of much extension, and a most interesting example is described in an article on the bubble chamber which is published elsewhere in this issue. The high pulse rate of some modern particle accelerators could have been stultified by purely practical difficulties, for data accumulated in a single day would take a year to analyse by existing methods, which demand the full attention of a skilled worker. But by means of a device in which the tracks revealed in a photograph are followed on a screen by crossed hairs, and the resulting movements are analysed by an information computer, the significant features of any collision can be determined in about a minute. This work can be carried out by an operator who has had little training, and the expert need give his attention only to those collisions which have been shown to possess points of interest.

Some scientists, and especially those brought up in an older tradition, view these changes with concern, and certainly their extensive introduction demands most careful consideration. Increasing use of apparatus whose primary function is rapidly to increase our factual knowledge may lead to a feeling that in science it is facts, rather than the principles which they enable us to formulate, that are of fundamental importance. It is true, too, that such apparatus has only limited powers of interpretation, and it is difficult to see how it could be made to take proper note of the exceptional, or even accidental, results from which great discoveries have so often stemmed. Again, it is argued that undue dependence on automatic devices may impair that manual dexterity which is so valuable a part of the equipment of the experimental scientist. Such misgivings are understandable, but it would be illogical to suppose that the immense developments which have taken place in science in recent years—which have completely changed its place in society—could be sustained without some radical changes in technique. It would be surprising indeed if methods appropriate for the conditions of half a century ago needed no revision now. Moreover, the relative importance of such considerations can be over-estimated, for the primary function of such innovations is not to reduce the scientist's working hours, but to enable him to devote a larger proportion of his time to original work, both practical and theoretical, for which his knowledge and training are essential. It is important to note that such devices would do nothing to diminish the rigour of scientific argument—which is vital to healthy progress—for their purpose is to collect information and not to interpret it.

If this argument is accepted it follows that there is strong reason for introducing automation into science with the same deliberate intent as in industry, but such a positive policy is not so far being widely followed. It is nevertheless worth noting that such a development offers one means of alleviating effectively the present grave shortage of scientific and technical manpower. It is widely prophesied that in the next half-century industrial leadership will pass to the nations which first realize and apply all the implications of automation. But today industry cannot flourish without science, and it may well be that the introduction of new methods of organizing scientific work is no less important than that of new methods of organizing industrial production.

Muscular contraction

H. E. HUXLEY

In recent years there have been considerable advances in our knowledge and understanding of the mechanism of muscular contraction. These have come from two main sources—from biophysical and biochemical studies of purified muscle proteins and of 'model' muscle systems of various types, and from investigations of the molecular structure of muscle and the changes in that structure which occur during contraction. The large-scale physiological properties of muscle are now beginning to find expression in structural and chemical terms.

Muscle may be considered as essentially a highly specialized machine, constructed from organic materials, which utilizes chemically stored energy and performs mechanical work. The existence of some such mechanism is indispensable to the directed movement of any biological system, and its speed and efficiency decisively influence the types of animal life which can exist. All machines arouse our curiosity, and this one is no exception; the question of how it works comes at once into our minds. This article will not answer this question, but it will attempt to summarize some of the evidence and arguments on which our present ideas about muscular contraction are based. These ideas, though fruitful in many respects, have one very great failing: they have not enabled us to decide what fundamental principle or property is involved in contraction. Non-biologists may be surprised that such an unsatisfactory state of affairs should prevail in so important a subject, but, in fact, our knowledge and understanding of muscle are probably more complete than they are of any other biological system. If the mystery of contraction remains unsolved for long, it will not be for want of experiment or thought.

GENERAL PROPERTIES OF MUSCLE

There are basically two different types of muscle. Voluntary muscles are quick-acting and exhibit a banded or striated appearance in the light microscope; this class includes the skeletal muscles used to produce body and limb movements in vertebrates. Involuntary muscles, such as those which produce intestinal movements, or the dilatation of the capillaries, are in general much slower in their operation, and they do not appear banded. The two types are usually referred to as 'striated' and 'smooth' muscles respectively. Cardiac muscle seems to occupy an intermediate position, for although not under voluntary control, its structure resembles that of striated muscle. The properties of smooth muscle have been studied a good deal less than those of striated muscle, and it is with the latter that we shall mainly be concerned.

A whole muscle is built up of a large number of individual fibres, which range in diameter from 0·01 to 0·1 mm and which may extend the whole length of the muscle. These fibres are electrically excitable, and they will contract when an electrical impulse is transmitted to them down the motor nerve. A single impulse produces a single contractile event, known as a twitch, whose duration is of the general order of magnitude of one-tenth of a second, though considerable variation exists between different muscles. A longer contraction, known as a tetanus, can be maintained by a continuous flow of impulses. When the impulses cease, contraction ceases too, and if the muscle has been allowed to shorten it may be re-extended by a very small force. The muscle is said to relax. Under normal physiological conditions muscles do not in general shorten to below 65 per cent of their resting length, nor stretch to more than about 140 per cent of their resting length. The normal range of operation is often even more restricted than this: 85 per cent to 120 per cent would be a typical figure. The tension exerted by a muscle is a maximum at resting length and decreases on either side of that length.

During a tetanus, a muscle can exert a tension of about 4–5 kg per square centimetre of its cross-section. The tension exerted is a function of the velocity of shortening [1]. Maximum tension is exerted when the muscle is not allowed to shorten at all, i.e. during an isometric contraction. If P_0 is the maximum tension that the muscle can exert at any particular length, then when it is shortening with velocity v the tension exerted will be P, where $(P + a)v = (P_0 - P)b$, a and b being constants for a given muscle. This is the well-known Hill equation. One feels that such a simple relationship

must reflect some very simple feature of the mechanism of contraction.

HEAT PRODUCTION

When one considers the production of heat by a contracting muscle, the above relationship takes on an even simpler form. The heat given out by a muscle during contraction may conveniently be divided into two parts: the initial heat, which always appears, whether the muscle is allowed to shorten or not; and the shortening heat, which appears when the muscle decreases in length [2]. No heat changes take place when the muscle relaxes and returns to its resting length. The amount of shortening heat is proportional to the distance the muscle shortens, and is independent of the tension being exerted during the shortening process. Moreover, the heat evolved for an amount of shortening x is found to be equal to ax, where the constant a has the same value as it does in the force-velocity equation. Thus, leaving aside the initial heat, the left-hand side of the force-velocity equation given above will represent the total rate of energy release (heat + work) by the contracting muscle. The equation therefore shows that this quantity is proportional to the difference between the maximum tension and the tension which is actually being exerted. This seems to be a very significant relationship.

ENERGY RELEASE

The fact that the amount of heat produced when a muscle shortens by a given distance is independent of the external work done by the muscle is most remarkable. A good many of the more straightforward mechanisms that might be suggested for contraction set free a constant total amount of energy when they shorten a given distance, and they would therefore predict a heat of shortening which increased as the external work decreased. But in muscle the total energy released in a given distance varies with the load, and it is always equal to the external work done plus a constant shortening heat. Moreover, this is an inherent property of the contractile material, and is not dependent on some feedback arrangement in the nervous system. In some respects the system resembles an electric motor drawing a larger current from the mains supply when its speed is decreased by an external load, though this analogy cannot be pursued very far.

The mechanism of contraction must clearly be of a very special kind. First of all, the chemical reaction which releases energy for contraction must be linked to a movement or change of shape in the molecular structure of the muscle. Secondly, this movement or change of shape must enable the muscle as a whole to shorten by at least one-third of its resting length. Thirdly, the amount of reaction which takes place must be determined by the external work done by the muscle and not by the distance it shortens. Fourthly, the mechanism must give the very simple force-velocity relation described by the Hill equation. Fifthly, after a contraction the muscle must be able to return to its resting length without any further heat changes taking place. Thus, even apart from its relevance to muscular contraction, it is of considerable intrinsic interest to try to discover how such a molecular mechanism can work.

APPROACHES TO THE PROBLEM

The properties of muscle which have been briefly outlined above are so striking and so clearly defined that one feels they ought to be explicable in fairly simple terms. An explanation can be sought in two rather different ways. The first approach is simply to try to see how a muscle is constructed. The large-scale structures can be studied in the light microscope; the details of the fine structure can be observed in the electron microscope or investigated by X-ray diffraction techniques. If the structure of the working parts of a muscle can be described in sufficient detail, then one should be very close to understanding how the mechanism operates.

The second approach is the biochemical one. Many of the components of a muscle can be extracted and purified, and their chemical and physical properties studied either individually or in combination with one or more other components. Systems can be set up—for instance, artificial fibres prepared from purified muscle proteins—which display some of the properties of living muscle, and whose behaviour can be studied under much more closely controlled conditions.

The two approaches can never be wholly separate, nor should they be; they differ much more in the way the information is obtained than in the type of information they ultimately seek. The correlation of the information obtained by the different methods not only helps to preserve an atmosphere of realism in the different disciplines but should eventually remove the boundaries between them, so that the same phenomena might equally well be described by a physiologist, a biochemist, or a physicist, each using terms which have a real meaning to the others. Before discussing the

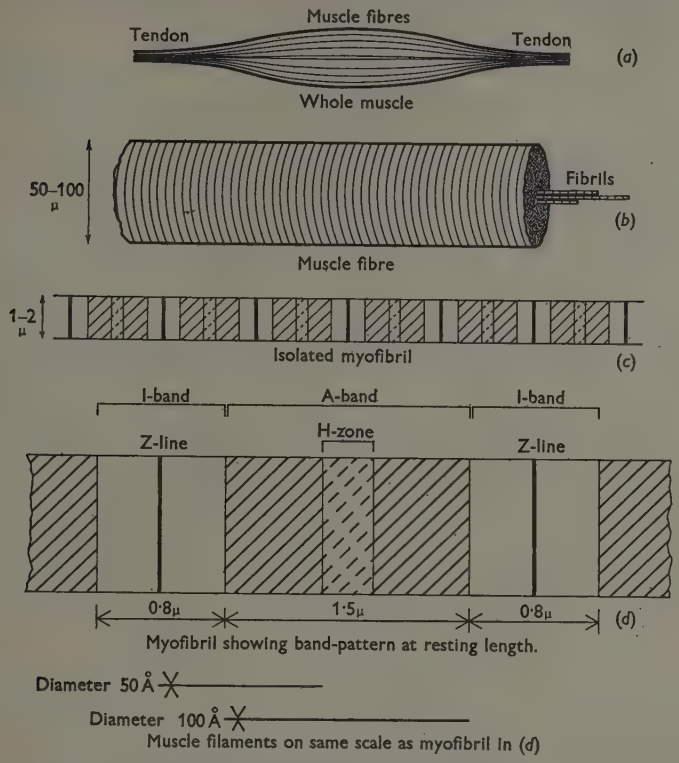

FIGURE 1 – *The structure of muscle at different levels of organization; dimensions shown are those for rabbit psoas muscle.*

contractile structure itself, however, brief mention should be made of the means by which the signal for contraction is transmitted into that structure.

MECHANISM OF STIMULATION

The muscle fibre is the smallest unit which will perform a normal physiological contraction. Each fibre is surrounded by a thin membrane which is electrically polarized and in the resting state has a potential difference of about one-tenth of a volt across it, the inside being negative. When the muscle is stimulated, via its motor nerve and motor end-plate, a wave of depolarization, the action potential, travels down the muscle membrane, with the result that the potential difference across it falls to zero and, in fact, overswings and reverses in sign. Almost immediately the muscle contracts. The depolarization of the membrane is known to alter its permeability to different ions, and it is natural to inquire whether the passage of some specific ion through the external membrane could trigger off the contraction. However, such an explanation is not tenable, at least in its simple form, for the muscle fibre becomes fully active across its entire cross-section in a much shorter time than such ions would take to diffuse to or from the centre of the fibre [3]. Recently it has been suggested [4] that the signal for contraction might be transmitted into the interior of the fibre at the requisite speed as a wave of depolarization in an internal transverse membrane. A system of such transverse membranes, spaced at short intervals along the fibre, and each releasing activator in the interior of the fibre when they were depolarized, would then provide the necessary speed of activation. Strong evidence has been produced [4] that such a mechanism does in fact exist in striated muscle.

THE CONTRACTILE STRUCTURE

The contractile material is located inside the muscle fibres in the form of thin longitudinal fibrils, called myofibrils, about 1 micron in diameter, packed close together across the width of the fibre and extending along its whole length. If the fibres are disrupted mechanically, for instance in a Waring blender, the individual fibrils are released. These isolated myofibrils provide a very important experimental material. Though they cannot, of course, be stimulated electrically, they can be made to contract by appropriate biochemical treatments; they seem to contain the essential contractile apparatus of muscle, still in a highly organized form, but free from the complicated and uncontrollable factors present in a whole living muscle.

The fibres of voluntary muscle are crossed by a regularly repeating pattern of bands; these cross-striations have a periodicity of the order of two or three microns at resting length. The period seems to be constant for a given type of muscle at resting length, but varies somewhat from one type of muscle to another; some muscles (e.g. the leg muscles of certain spiders) have exceptionally long striations. This banding is a property of the myofibrils, which are arranged in the fibre with their striations in register. The pattern is shown in figure 1, and figure 3(*a*) (page 185) shows an individual myofibril photographed in phase-contrast illumination. The principal feature is the succession of alternating dark and light bands,

which correspond to dense and less dense regions of the myofibril. The dense bands are birefringent and are known as the A (anisotropic) bands; the less dense bands are relatively non-birefringent and are known as the I (isotropic) bands. The I-bands are bisected by a dense line, known as the Z-line or Z-membrane. The Z-membranes appear to be continuous across the whole width of the fibre and to hold the fibrils in register; there is evidence [4] that they may provide the path along which the signal for contraction is transmitted into the interior of the fibre.

This pattern has been described in some detail, for its features are not of merely morphological interest: they are the visible expression of the highly organized molecular structure responsible for contraction; they are related to that structure in a remarkably simple way; and once that relationship has been recognized they can give very specific information about the nature of the molecular changes taking place during contraction.

STRUCTURE VISIBLE IN THE ELECTRON MICROSCOPE

When muscle is examined in the electron microscope it is found that the myofibrils themselves are built up of smaller longitudinal filaments having diameters of the order of 100 Å. These filaments remain straight when the muscle contracts. They form a continuous array across the whole width of the myofibrils, being spaced out a few hundred Ångström units apart; in life, the space between them is filled with a solution of salts and soluble proteins. The array of filaments is quite crystalline in its regularity, and living muscle will reflect X-rays quite strongly at the appropriate angles [5].

Within the last few years, technical developments have made it possible to cut sections of muscle and other biological tissues which are sufficiently thin to be examined in the electron microscope. This has greatly extended the range of usefulness of the instrument, and, because of the extreme thinness of the sections (only one or two hundred Ångström units), has made it possible to achieve resolution of the order of 30 Å on biological material. Examination of electron micrographs of very thin cross-sections of muscle reveals some remarkable features about the structure [6]. Cross-sections through the denser parts of the A-band (i.e. the regions on either side of the H-zone) show that two different types of filaments are present here (figure 4(*a–e*)). First there is a hexagonal array of 'primary' filaments about 100 Å in

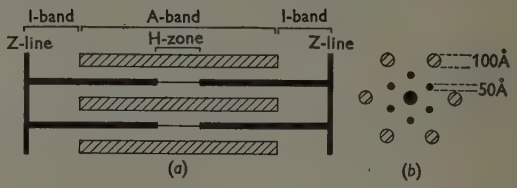

FIGURE 2 – *Diagrammatic representation of arrangement of filaments in striated muscle:* (a) *longitudinal*, (b) *sectional.*

diameter and spaced about 200–300 Å apart. The spacing as measured by X-ray diffraction in living muscle is 450 Å, and the lower value seen here is probably due to shrinkage during the preparation of the material for sectioning. Between the primary filaments a secondary array of thinner filaments, about 40–50 Å in diameter, can be seen; each secondary filament lies symmetrically between three primary filaments, so that each primary filament has around it six secondary filaments which it shares with its six nearest neighbour primary filaments. The arrangement is shown diagrammatically in figure 2.

Sections through the central region of the A-band, the H-zone, show only the hexagonal array of primary filaments (see figure 4(*f*)), and any secondary filaments in this region must be so thin as to escape detection. Sections through the I-band show only thin filaments of diameter about 50 Å, and the hexagonal array of primary filaments is not present in this band, as indeed is obvious from longitudinal sections (see figure 3(*b*)).

The conclusion from these observations is a very straightforward one. It is simply that the fibrils are built up of two overlapping, interpenetrating arrays of longitudinal filaments (figure 2). The thick filaments are confined to the A-band and produce the high density and birefringence of that band. Thin filaments extend in either direction from the Z-line, through the I-band, into the A-band, and terminate or become much thinner at the edge of the H-zone. The densest zone of the band pattern occurs where the two arrays of filaments overlap, i.e. in the region of the A-band on either side of the H-zone. The next densest zone occurs where the thicker filaments are present on their own, i.e. in the H-zone. The least dense band occurs where thin filaments alone are present, i.e. in the I-band, for although there are twice as many of them as there are thick filaments, the cross-sectional area of each one of them is only about one quarter as great.

We see then that the visible striated appearance

of skeletal muscle arises directly from the organization of the contractile material of the myofibrils into two distinct, overlapping arrays of filaments.

BAND PATTERN CHANGES DURING CONTRACTION AND STRETCH

The A- and I-bands have lengths of the order of one micron. Thus in the physiological range of contraction the changes in band length can be only fractions of a micron. Such small changes are difficult to measure, particularly when they are taking place very rapidly, and the measurements are very susceptible to optical artifact. Fixing the muscle prior to examination in the light microscope or the electron microscope does not really solve the problem, for the fixation process may itself introduce changes in band length. It is only in the last few years, with the introduction of the phase-contrast and interference microscopes, that accurate and dependable measurements have become technically possible [7, 8]. The results are remarkably simple. Consider, for example, skeletal muscle from the rabbit or the frog. At resting length, the distance between successive Z-lines, which defines the repeating period of the cross-striations, is 2·3 microns; the length of the A-band is 1·5 microns and that of the I-band 0·8 micron. When the muscle contracts, the A-band remains at constant length, and the I-band decreases in length until it disappears altogether at about 65 per cent of the resting length. This is the normal limit of physiological contraction, and further shortening beyond this point produces dense contraction bands where adjacent A-bands have been brought into contact at the Z-line. In figures 6 and 9 these changes are illustrated both diagrammatically and as they take place in a single muscle fibril observed in the phase-contrast microscope.

If relaxed muscle is stretched, the A-bands remain at constant length and the increase in length is taken up by the I-bands. During contraction from a stretched condition the same process happens in reverse. During an isometric contraction, when the muscle exerts a force but is not allowed to shorten, neither the A- nor the I-bands change in length. It appears that under all conditions the band pattern is determined simply by the length of the muscle, and is the same whether the muscle is in the active state or not. Moreover, the same band pattern changes are observed in experiments both on living fibres contracting under normal physiological conditions and on isolated fibrils made to contract by biochemical means.

One further, and most illuminating, feature of the band-pattern changes should now be described. It will be recalled that the central region of the A-band, the H-zone, is somewhat less dense than the regions on either side of it. When the muscle increases in length, the H-zone increases in length by the same amount, although the total length of the A-band remains constant. Thus the distance from the Z-line to the edge of the H-zone remains constant (see figure 8). The appearance of a stretched fibril, with its very long H-zone, is shown in the electron micrograph reproduced in figure 7. During shortening, the H-zone decreases in length until it disappears at about 85 per cent of the resting length; it is replaced by a dark line if further shortening occurs.

These observations have a very simple explanation, which becomes particularly obvious when the electron microscope observations are kept in mind. It is that the two arrays of filaments, whose lengths define the length of the A-band and the distance from the Z-line to the edge of the H-zone, always remain, so far as possible, at constant length, and that changes in the length of the muscle are brought about simply by the two arrays sliding into or out of each other [7, 8]. If the muscle contracts too far, the filaments of one or of both arrays will have to crumple up at the ends for steric reasons, but over a considerable range of lengths the sliding process alone takes place. Additional support for this hypothesis is provided by the X-ray diffraction data.

X-RAY DIFFRACTION EVIDENCE

The filaments seen in electron micrographs of muscle often show a longitudinal periodicity of about 400 Å, and a similar axial period (415 Å) has been demonstrated in low-angle X-ray diffraction diagrams obtained from living muscle [5]. The X-ray reflections are very sharp and show that the periodicity must be maintained with almost atomic precision. When a living muscle is stretched, the X-ray period does not increase, and diagrams obtained from artificially contracted muscle suggest that the period remains constant there too. It is not clear at present whether the X-ray period arises from the internal structure of only one type of filament or of both types. However, whichever is the case, the X-ray evidence shows that the structure which gives rise to the 415 Å axial period does not change in length when the muscle changes in length. This result is in perfect accord with a sliding-filament model.

No characteristic changes associated with contractions have been observed in the wide-angle

X-ray diagram given by muscle [9]. This again shows that the major part of the internal structure of the filaments retains a constant atomic configuration during contraction.

From the light microscope and electron microscope evidence, and from the X-ray data, the conclusion seems inescapable that contraction is brought about by some mechanism which causes the two different types of filament to slide past each other. We must now inquire what is the composition of these filaments, and what interactions between them might cause such a sliding process to occur.

THE PROTEIN COMPONENTS OF MUSCLE

Muscles contain about 20 per cent of protein and 80 per cent of dilute salt solution. About two-thirds of the protein is present in fibrous form and constitutes the contractile structure of the muscle. Other proteins present include enzymes for facilitating reactions which convert the energy-rich compound glycogen from the bloodstream into another compound which can be used directly as an energy source by the contractile machinery. These metabolic reactions synthesize adenosine triphosphate (ATP), and it has long been realized that the hydrolysis of this compound to adenosine diphosphate (ADP) was a reaction very closely linked to the contractile process. Although this reaction can be demonstrated as taking place in contractions of appreciable duration, attempts to demonstrate any breakdown of ATP during a single twitch have not been successful [10, 11]. It remains in doubt, therefore, whether some other compound, itself synthesized from ATP, might not be the immediate energy source, or even whether the contractile mechanism might not itself be able to perform one twitch without an external supply of energy.

The two great simplifying discoveries in muscle biochemistry which have enabled thought and experiment to be directed at the real essentials of the problem of contractility are concerned with the structural proteins. Two of these, actin and myosin, are of special importance and together make up about half the total protein in muscle. Myosin had for a very long time been recognized as a typical fibrous protein, and it was generally believed that some change in the configuration of the myosin molecule was the factor responsible for muscular contraction. It was a considerable sensation, therefore, when the discovery was made [12] that myosin is itself the enzyme which catalyses the breakdown of ATP to ADP.

Perhaps even more dramatic still was the discovery that artificial fibres made from a mixture of actin and myosin extracted from muscle will contract when they are placed in a suitable solution containing ATP [13, 14]. These discoveries showed that the entire basic mechanism of contractility is contained in the actin-myosin-ATP system.

PROPERTIES OF MYOSIN AND ACTIN

Myosin has a molecular weight often reported to be 800,000 (see, for example, [15]), but is now reported as being only half that value [16]. The molecule is long and thin, and light-scattering and other measurements [15, 17] give a length in the range 1500–2000 Å, with a diameter of about 20 Å. Actin has a molecular weight of about 70,000 [15], but its shape is uncertain. It can exist in solution in two different forms. One form is known as globular or G-actin, and seems to consist of either single molecules or dimers. When salt is added to solutions of G-actin, another form, known as fibrous or F-actin, is produced. One might therefore expect the actin in muscle to be present as F-actin. Solutions of F-actin have a high and anomalous viscosity, exhibit strong flow-birefringence, develop birefringence spontaneously on standing, and display many other characteristics to be expected of long polymers of G-actin units. They have two very interesting features. If actin is labelled with a fluorescent dye, then the rotational periods of the G-actin units in F-actin can be calculated from measurements of the depolarization of fluorescent radiation. These measurements lead to the conclusion that the G-actin units in fibrous actin have freedom of rotation about at least one axis [18]. It is also found that globular actin has ATP bound to it, and that the ATP is transformed into ADP when G-actin polymerizes to form F-actin [19].

When solutions of actin and myosin are mixed together, the viscosity of the mixture is considerably higher than the sum of the viscosities of the constituents. If the mixture is centrifuged at high speed, almost all the protein forms a compact pellet of sediment, whereas under similar conditions myosin on its own would remain largely in the supernatant [20]. It is clear that some sort of complex can form between actin and myosin; this is known as actomyosin. If ATP is added to a solution of actomyosin in 0·6 M. KCl, a large fall in viscosity occurs, and myosin, and only myosin, can be recovered from the supernatant left after a degree of centrifuging that would bring down

actomyosin and F-actin [20]. It seems, then, that at this salt concentration, ATP dissociates the actomyosin complex into actin and myosin; ATP is itself split by myosin, and when all the ATP has been hydrolysed in this way the actomyosin complex reforms. At lower salt concentration (e.g. 0·1 M.) ATP brings about the precipitation of actomyosin from solution. And when the actomyosin has been orientated into threads, ATP produces contraction.

If the actin molecules are labelled, as before, with a fluorescent dye, they will still form actomyosin; fluorescence depolarization measurements show that the actin units in actomyosin behave as monomers having freedom of rotation about at least one axis; when actomyosin is dissociated by ATP, the actin immediately behaves as though it were composed of dimers [21]. These are all fascinating and rather baffling relationships, and no comprehensive scheme that will explain all of them has yet been evolved.

MODEL SYSTEMS

The inter-reaction between actin, myosin, and ATP can also very profitably be studied in model systems which lie in their complexity part-way between the purified protein solution and the living fibre. The first of these, the actomyosin thread, has already been mentioned. The second is the so-called glycerol-extracted fibre model. It was found by Szent-Györgyi [22] that muscle fibres which had been kept cold in 50 per cent glycerol for a few days or weeks would, though of course no longer electrically excitable, contract when placed in suitable solutions containing ATP. It has been found that this contraction imitates in very many respects the contraction of a living fibre, although it takes place more slowly. The maximum tension exerted is roughly the same.

The glycerinated fibres are normally inextensible and resemble muscle in rigor, for they have lost the ATP which fresh, living muscles contain. If, after an ATP-induced contraction, the ATP is washed out of such a fibre model, then the fibre 'sets' at the shortened length. If, however, the dephosphorylation of ATP is inhibited either by an enzyme poison, for instance salyrgan, or by a factor [23] which can be extracted from fresh muscle, then not only is contraction abolished, but the fibre may now be readily re-extended to its original length. Under these conditions ATP is said to act as a plasticizer.

Certain inorganic phosphates, as for instance sodium pyrophosphate [24], also produce a plasticizing effect on glycerinated muscle; these compounds are not dephosphorylated by myosin, but they all have the property of lowering the viscosity of an actomyosin solution; so, like ATP, they can presumably dissociate the actomyosin complex.

These observations may be compared with the behaviour of living muscle fibres. These contain ATP, but in the resting state the enzymatic activity of myosin is inhibited in some way and ATP breakdown is very slow; the fibres are quite flexible and may be stretched easily. During contraction the muscle becomes quite rigid, but regains its plasticity when the contraction is over. If the muscle is allowed to pass into rigor, a condition associated with the loss of ATP, then the fibres will no longer contract, and they become rigid and inextensible.

It seems, then, that ATP performs a dual role in muscle. When dephosphorylation cannot take place, the presence of ATP keeps the muscle plastic and extensible; when dephosphorylation can take place, the presence of ATP causes contraction.

BIOCHEMICAL CONCLUSIONS

We may summarize the biochemical evidence as follows:

1. The contractile structure is built largely out of two proteins, actin and myosin.
2. Some sort of combination can occur between actin and myosin.
3. This combination is modified by the presence of ATP.
4. Myosin is an enzyme for the dephosphorylation of ATP.
5. The dephosphorylation of ATP is very closely linked with the release of energy for contraction.
6. The presence of ATP without dephosphorylation makes the contractile structure extensible.
7. Other substances which, like ATP, dissociate actomyosin, also make the contractile structure extensible.
8. In the absence of ATP or other plasticizer the contractile structure becomes rigid and inextensible.

Let us now see what expression these concepts find in our structural knowledge of muscle.

THE PROTEIN COMPOSITION OF THE FILAMENTS

Myosin can be dissolved out from either whole muscle or from isolated myofibrils by procedures

which remove little or no actin [25]. Microscopic observations [26, 27] show that the removal of myosin is associated with the extraction of the dense material of the A-bands, i.e. of the so-called A-substance. This is illustrated in figure 5, which shows an isolated myofibril before and after myosin has been extracted from it. A 'ghost' fibril is left, consisting of material extending from the Z-lines to the edge of what was formerly the H-zone; the H-zones now have a very low density, but the fibril structure is still continuous across them. The ghost fibrils will not contract in solutions containing ATP. In the electron microscope it can be seen that the array of thick filaments which characterized the A-bands of normal muscle is no longer present. Moreover, quantitative measurements made with the interference microscope [28] show that the amount of A-substance, present in intact fibrils and removed from them when myosin is extracted, is exactly equal to the myosin content of the fibrils given by biochemical analysis. One can conclude, therefore, that the thick filaments seen in the electron microscope in the A-bands of muscle are made up very largely of myosin.

After myosin has been removed from muscle, actin can be extracted by another procedure. When the ghost fibrils remaining after myosin extraction are treated in the same way, then most of the residual material between the Z-line and the edge of the H-zone is removed (see figure 5). It will be remembered from the account of electron-microscope observations that this material consists of the thin filaments which formed the secondary hexagonal array where they overlapped with the thick filaments in the A-band. Thus one must conclude that these secondary filaments contain the protein actin.

One arrives, therefore, at the very simple concept that the two principal contractile proteins of muscle, actin and myosin, are organized into separate filaments; and that the interaction of actin and myosin filaments with ATP causes them to slide past each other (figure 10). It is in the light of this model that a relation should be sought between the biochemical observations and the physiological behaviour of muscle.

CORRELATION OF STRUCTURE, BIOCHEMISTRY, AND PHYSIOLOGY

The construction of striated muscle in this particular fashion would appear to offer two advantages from the mechanical point of view. These arise from the two basic features of the structure—the discontinuous nature of both the actin and the myosin filaments, and the fact that groups of filaments of any one type are arranged in register. In the first place, a considerable amount of shortening can take place without either type of filament having to fold up in any way. Secondly, the filaments within any given array do not move relative to each other, and so internal frictional losses will be kept at a minimum. The arrangement looks neat, efficient, and well adapted to carrying out rapid contractions [29].

A good starting point to show the way in which the different types of information about muscle are beginning to fit together is provided by the behaviour of muscle when it is stretched. During stretch we have seen that the actin filaments are drawn further out of the array of myosin filaments. If cross-links were to be formed between the actin and the myosin filaments, then, if the filaments themselves were inextensible, the muscle too would be inextensible. Such cross-links would correspond to the combination that can take place between actin and myosin in solution. ATP is believed to dissociate this combination, and one might therefore expect it to break the cross-links between actin and myosin filaments. Thus the observation that muscle and muscle models are extensible only in the presence of ATP, or of other substances which can dissociate the acto-myosin complex, can be accounted for in an extremely simple way.

CONTRACTION MECHANISMS

The picture of contraction which has now emerged may be summarized as follows.

In the resting state, the two overlapping arrays of filaments are not linked to each other because of the presence of ATP and the absence of ATP breakdown. When the muscle is stimulated, the release of some activator allows the enzymatic breakdown of ATP to commence. An interaction between myosin, actin, and ATP takes place and, as a result, the array of actin filaments is drawn further into the array of myosin filaments, producing shortening of the muscle and the observed change in band pattern. When ATP breakdown ceases, its interaction with myosin and actin no longer produces contraction but simply breaks the links between the two filaments; the muscle can then be re-extended. In the case of a glycerinated fibre the process is similar, except that ATP breakdown, and contraction, begin as soon as ATP is supplied to the fibre, and finish only when ATP is washed out of the fibre, leaving it locked at its

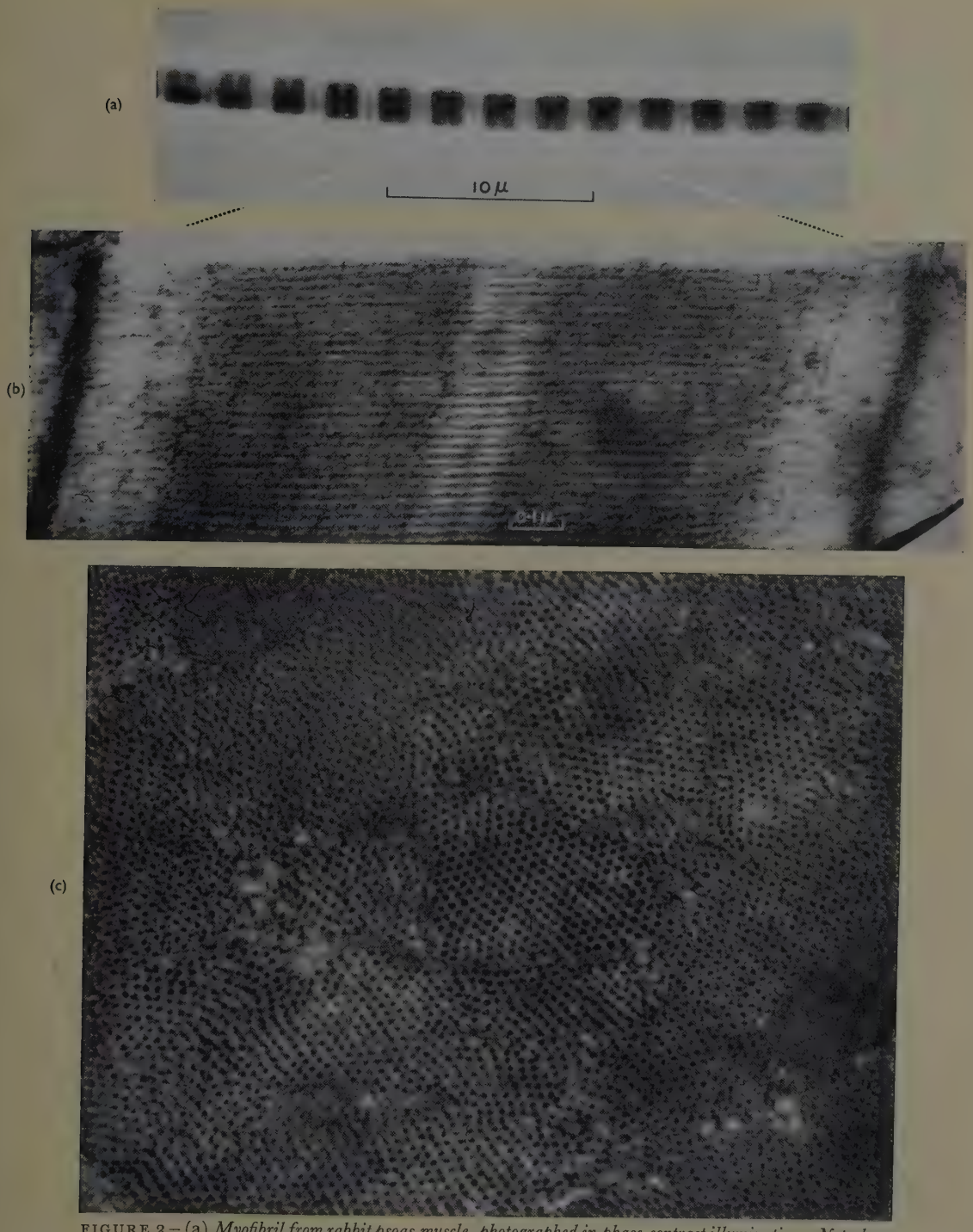

FIGURE 3 – (a) *Myofibril from rabbit psoas muscle, photographed in phase-contrast illumination. Note dense A-bands; the I-bands are less dense and are bisected by the Z-lines.* (b) *Ditto, as seen in electron microscope (longitudinal section).* (c) *Cross-section of muscle, showing the continuous array of filaments; in the centre of the picture the section has passed through an H-zone and a simple array is visible; on either side the compound array present in the rest of the A-band may be seen.* (*Magnification as* 3(b).)

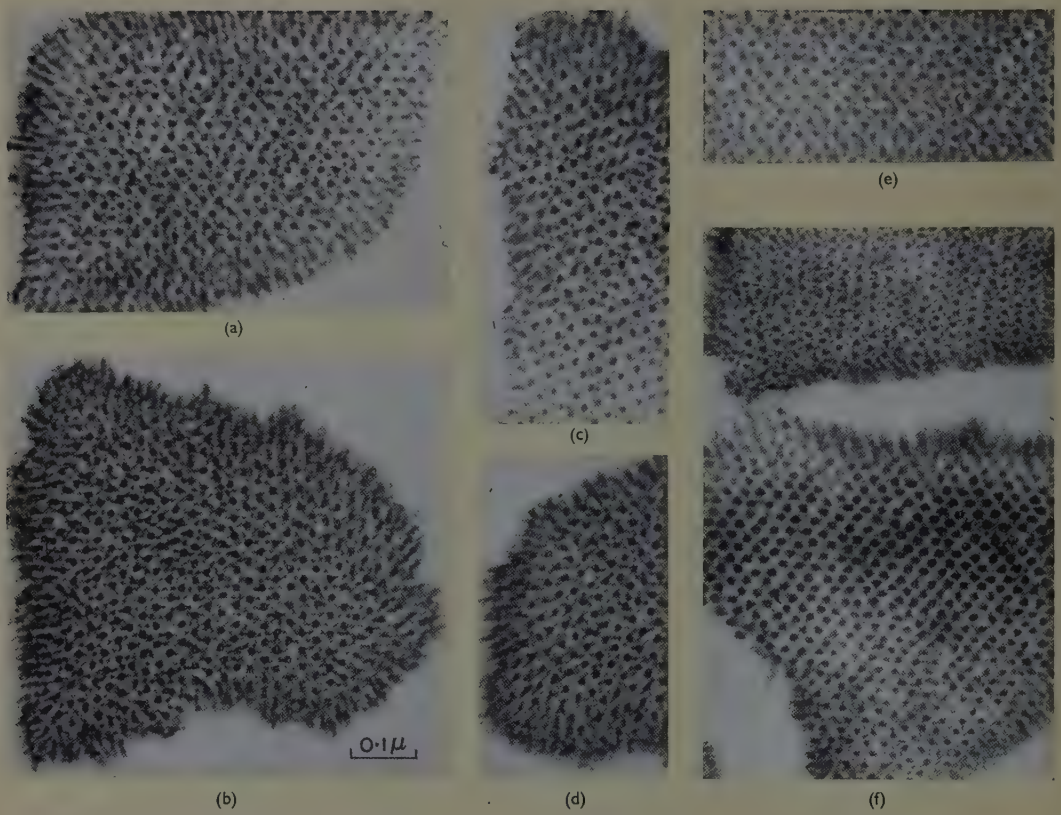

FIGURE 4 – *Electron micrographs of cross-sections of rabbit psoas muscle (stained with osmic and phosphotungstic acids). (a–e) Sections showing double hexagonal array of filaments in the A-band.* (f) *Sections showing simple hexagonal array of filaments in the H-zone.*

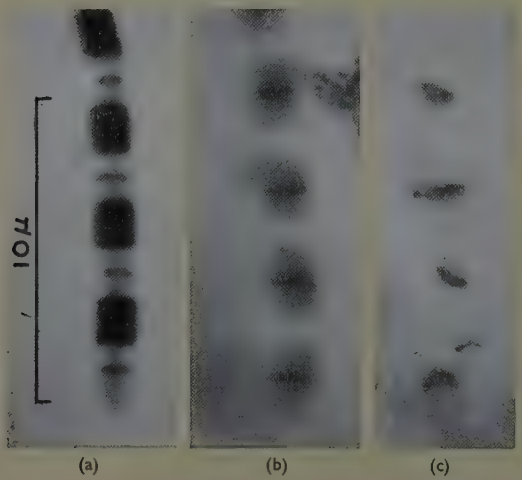

FIGURE 5 – *Extraction of proteins from myofibril:* (a) *before extraction;* (b) *after extraction of myosin (note removal of A-substance);* (c) *after extraction of actin; only Z-lines and some backbone material remain.*

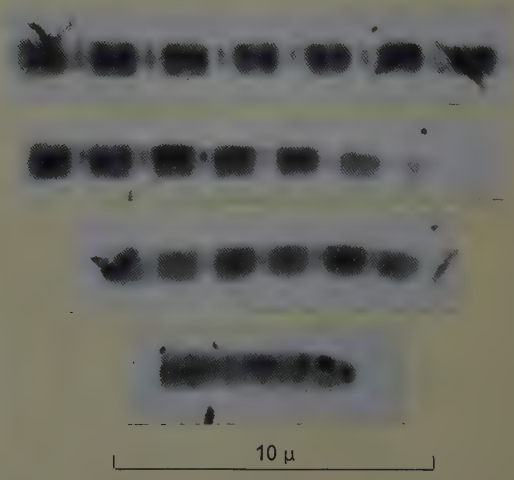

FIGURE 6 – *Myofibril from rabbit psoas muscle, photographed in phase-contrast illumination at successive stages of an ATP-induced contraction. Note shortening of I-bands and disappearance of H-zones.*

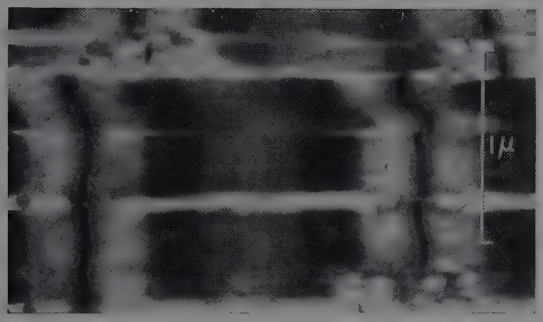

FIGURE 7 – *Electron micrograph of longitudinal section of stretched muscle; note long H-zones.*

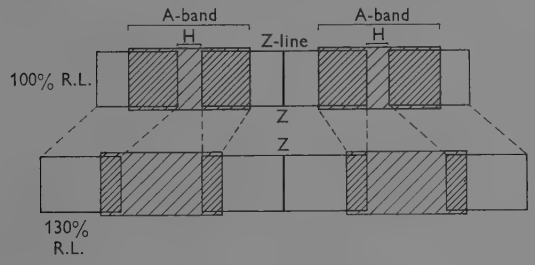

FIGURE 8 – *Diagram of band-pattern changes during muscle stretch; the distance from the Z-line to the edge of the H-zone remains constant.* R.L. = *Resting length.*

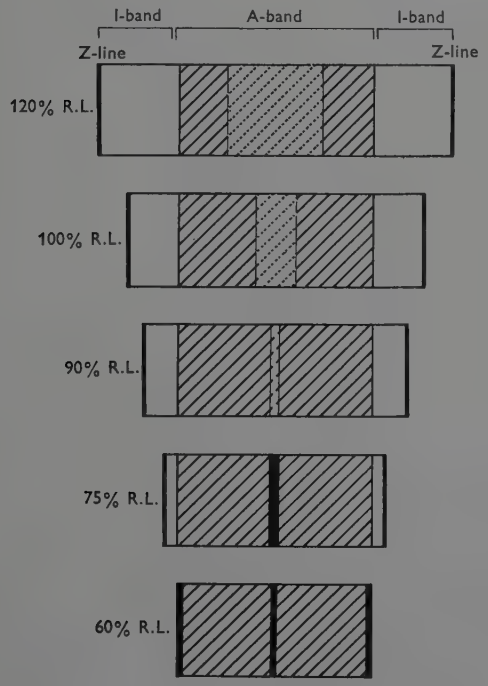

FIGURE 9 – *Diagrammatic representation of band-pattern changes during contraction.*

shortened length. The essential feature is that actin filaments are made to slide past myosin filaments by a reaction in which the dephosphorylation of ATP is involved but the details of which remain unknown. This feature sheds new light on a number of aspects of muscular contraction, which we will now consider briefly.

Each filament contains several hundred actin or myosin molecules. The X-ray diffraction evidence shows that in at least one type of filament, and perhaps in both, the molecules form a regularly repeating pattern. In the region where the two arrays of filaments overlap, myosin-actin interactions are likely to take place at a large number of points where actin and myosin molecules come into apposition. These interactions cause the two filaments to slide past each other. Each time the filaments move relative to each other by a distance equal to their axial periodicity, then virtually the same spatial pattern of interactions between them will recur. One might therefore expect the system to work in a step-by-step fashion, each complete contraction of the muscle being brought about by the repetition of a number of identical contractile events at the sites of myosin-actin interaction.

A possible mechanism could consist of obliquely oriented cross-linkages extending from the myosin molecules on one filament to the actin molecules on the other; the cross-linkages could form part of the myosin molecule itself. Shortening of the link would pull the actin filament along a short distance. The link could then be detached from the actin molecule (say by the arrival of a molecule of ATP), re-extend again, attach to the actin filament a little further along, and the whole process repeated. A more complicated mechanism involving repetitive alternations in length of the actin filaments has also been discussed.

Whatever the details of the mechanism, however, the same basic property remains: a number of minor cycles of a detailed molecular process take place within the major cycle of contraction and relaxation of the muscle itself. Thus one cannot simply equate the return of the muscle to its resting length with the re-extension of the contractile material; thus arguments about whether muscle as a whole relaxes actively or passively, though very important in many other respects, have no direct relevance to the question whether the contractile material extends actively or passively at the molecular level. Another feature of this type of mechanism is that each enzyme site—that is, each myosin molecule—can take part in the reaction a large number of times during each

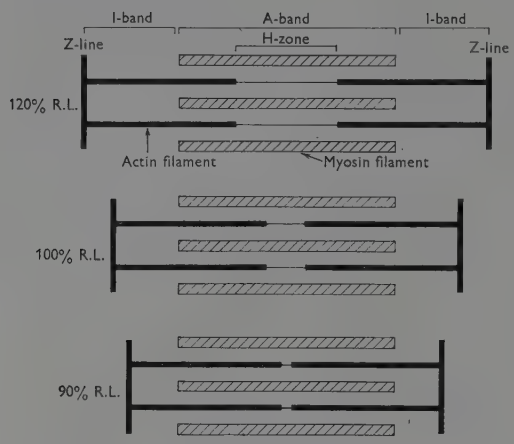

FIGURE 10 – *Diagram showing behaviour of actin and myosin filaments during changes of muscle length.*

overall contraction cycle. The total work done per cycle will therefore be much greater than in a system where each link can shorten only once per cycle, as for instance would be the case if the shortening of a number of links were added up in series.

A system of links, acting in parallel and having to break and reform each time a small amount of shortening takes place, has another interesting property. If a finite time is required for each link to form, then the number of links in existence at any particular moment, and hence the total tension exerted, will be a function of the speed of shortening. If the system is prevented from shortening, then there will be time for the maximum possible number of links to form, and the tension will be a maximum. Making a small number of assumptions, it can be shown that in such a system the rate of energy release varies with load in a manner which imitates closely the simple and striking behaviour of muscle itself [30].

The observations lead, then, to a mechanism whose general behaviour fits in very well with the physiological properties of muscle. The basic nature of this mechanism, however, still remains unknown. We still require electron micrographs which show the internal structure of the filaments and the details of any cross-connections between them; the details of the X-ray diffraction diagrams remain uninterpreted; and the actin-myosin-ATP interaction has still to be described in detailed terms. There is every hope that, along these lines, the problem of muscular contraction can be solved.

ACKNOWLEDGMENT

I am much indebted to my colleague Dr Jean Hanson; many of the ideas discussed in this article were the outcome of our collaboration, and the light-microscope photographs shown are taken from our joint publications. Many similar ideas have been developed by A. F. Huxley and R. Niedergerke.

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Edmond Halley (1656–1741)

SIR EDWARD BULLARD

To his contemporaries, and for a long time after his death, Halley was the 'second most illustrious of Anglo-Saxon philosophers'. Today most people know that he predicted the return of the comet of 1682 and that he persuaded Newton to write the *Principia*, but his own most original work has gradually been forgotten. The three hundredth anniversary of his birth on 29th October 1656 provides an appropriate occasion to look again at the life and work of a truly great man of prodigious versatility and most attractive personality.

Halley was the son of a prosperous London soapboiler.[1] When nearly seventeen years of age he went to The Queen's College, Oxford. While there he conceived a plan for making a catalogue and map of the southern stars. With characteristic impetuosity he left Oxford without taking a degree, and with the help of Sir Jonas Moore, the Master of the Ordnance, obtained a letter from the King recommending the East India Company to transport him and a friend to St Helena. On arrival Halley found the island to be almost continually covered by cloud, and consequently had great difficulty in obtaining the necessary observations during the year he was there. The results were published in 1679 in a catalogue giving the positions of 341 stars; the map shown in figure 2 was also published at about the same time. In addition he observed a transit of Mercury across the disc of the sun. He realized that this constituted a powerful method of determining the solar parallax and it is noticeable that throughout his life returned again and again to the subject, particularly recommending the observation of the transit of Venus which would occur in 1761. At St Helena he noticed that he had to shorten the pendulum of his clock to make it keep time; this had previously been observed by Richer at Cayenne, but these experiments were not known to Halley.

When Halley returned to Oxford he found himself in a difficulty which is not uncommon today. He had done an excellent piece of original work, but had not done it in Oxford and had not fulfilled the University's requirements for a degree. The Provost of his college was anxious to help him, but expected 'to find opposition among the Masters, who are difficult both to remit exercises and to give time'. Fortunately Halley had powerful friends who procured a letter from the King recommending to the Vice-Chancellor that he be given the degree of M.A. 'without performing any previous or subsequent exercises'.

The journey to St Helena was of critical importance in his career. On it he made his first substantial contributions to knowledge, and in connection with it he became known to the King and to several others who were eminent in science and politics. In 1678, soon after his return, he was elected a Fellow of the Royal Society. It was probably also this voyage that awakened his interest in the sea and started the stream of ideas on hydrography, diving, the winds, terrestrial magnetism, and the saltness of sea water, which occupied his most fruitful years.

After his catalogue of the southern stars was published he spent two years travelling on the continent. First, in 1679, he visited the aged Hevelius at Danzig and attempted to resolve the acrimonious dispute with Hooke about the relative merits of open and telescopic sights on astronomical instruments. Though Halley remained convinced of the superiority of the latter he failed to convince Hevelius, and was surprised to find that observations with open sights were often reproducible to 10 seconds of arc. He succeeded in staying on good terms with both disputants.

When he got home from his travels Halley was 25 years of age. A few months later he married Miss Mary Tooke, of whom almost nothing is known except that she was 'a young lady equally amiable for the gracefulness of her person and the beauties of her mind, in whose society he lived happily for fifty-five years' [3]. He seems then to have had no need to earn his living and decided to devote his time to astronomy. During the next three years he started a series of observations designed to last for 18 years, to correct the tables of the moon. Such a lengthy project was ill suited

[1] E. F. MacPike [1, 2] has collected and published most of the available information about Halley; in view of this, references are not given here for statements whose origin can be traced in MacPike's books. The most detailed life of Halley is that in the 'Biographia Britannica' [3].

to his temperament, and he was soon diverted to other things.

In 1684, when he was 27, he visited Cambridge to see Newton, then aged 43, and asked him whether he could prove that a planet would move in an ellipse if the sun attracted it with a force proportional to the inverse square of the distance. Newton said that he had proved this some time before, but could not lay his hand on the paper and would send it later. A few days later he sent two proofs. Halley fully realized the importance of what Newton had done, and with great skill and tact drew him on to develop his ideas, to communicate them to the Royal Society, and to publish them in 1687 in the *Principia*. The story is well known and is told by all biographers of Newton; here it is sufficient to say with De Morgan that 'but for him, in all human probability, that work would not have been thought of, nor when thought of written, nor when written printed.' Halley saw the book through the press, paid for the printing, and wrote the prefatory Latin verses.

It is clear from many expressions in his letters that Halley had a profound respect and devotion for Newton, and on many occasions went to considerable pains to help him. For example, in 1695 he offers to reduce Flamsteed's observations of the comet of 1680 'being desirous as far as you will permitt it, to ease you of as much of the drudging part of your work as I can, that you may be better at leisure to prosecute your noble endevours'. On first seeing the manuscript of the first book of the *Principia* he calls it 'your incomperable treatise', the third book is 'your divine treatise' [5], and nearly forty years later he calls Newton 'the person in the Universe I most esteem'.

In 1686 Halley had become Clerk, or what would now be called Assistant Secretary, to the Royal Society. The portrait of him that hangs in the room of the present Assistant Secretary was painted at about this time; it is reproduced in figure 1. He held this position for thirteen years. During this time he carried on a large part of the correspondence of the Society and attended almost all meetings both of the Society and of the council. He edited the Transactions and undertook to write five sheets in every twenty. He took part in discussions on the most diverse subjects and is recorded in the journal book as having spoken at twenty-six meetings during 1691. In 1692 he is known to have written or spoken on the measurement of the speed of ships, terrestrial magnetism, the origin of springs and rivers, diving bells, the methods of making diving suits watertight, the grinding of telescope mirrors, the flow of water from a hole in a vessel, the invention of an instrument which is a forerunner of the modern marine sextant, the size of objects seen under water, a support for a compass needle, the accuracy of his observations at St Helena, a possible slowing of the moon in its orbit revealed by ancient eclipses, a method of moving excavated earth, the prediction of eclipses, the design of a coelostat, lunar theory and methods of observation, a method of securing a ship's guns in bad weather, and 'the figure of the Caepia'. This flow of ideas, inventions, and experiments continued for years. Some of the subjects are a little trivial, but many are of the highest originality, ingenuity, and interest. Perhaps the most striking of his investigations at this period are two papers in the Transactions for 1683 and 1692 respectively [6] on the variation, or, as it is now called, the declination, of the magnetic compass.

In the first paper Halley collects 55 observations taken between 1580 and 1682 at 47 different places. He uses these to refute Gilbert's suggestion that the variation is due to the attraction of the north pole of the needle by the magnetized masses of the continents and Bond's suggestion that it can be accounted for by the attraction of a dipole inclined to the earth's axis of rotation. Another suggestion, due to Descartes, ascribed the variation to masses of iron and lodestone. Halley points out that, although there undoubtedly are local attractions, the main features of the variation are of continental extent '*ex. gr.* in the whole Indian Sea, the Needle declines the same way, and that regularly, 'twill follow that the attracting Substance that occasions it, must be very far distant.' In his first paper Halley suggests that four poles in the Arctic regions are sufficient to account for the observed variation all over the world. The arguments are qualitative, since 'to calculate exactly what it is, in any Place assign'd, is what I dare not yet pretend to', since observations are few and many of them of doubtful accuracy, 'and besides, it remains undetermin'd in what proportion the attractive Power decreases, as you remove from the *Pole* of a Magnet, without which it were a vain Attempt to go about to calculate'. A few years later Halley made some experiments in the courtyard of Gresham College with 'the Society's great magnet'. These experiments give a good indication of an inverse cube law, but Halley seems never to have referred to them again, perhaps because they gave the variation of force

with distance outside the magnet and not the variation over the surface, which was what he needed.

In the second paper Halley considers the secular change of the declination. By many examples he shows that the phenomena 'do sufficiently evince, that the whole Magnetical System is by one, or perhaps more motions translated . . . that this moving thing is very great, as extending its Effects from Pole to Pole, and that the Motion thereof is not *per saltum*, but a gradual and regular Motion' westward. He points out the great difficulty that this raises for all theories of terrestrial magnetism; for 'considering the Structure of our Terraqueous Globe, it cannot be well suppos'd that a very great part thereof can move within it without notably changing its Center of Gravity and the Equilibre of its Parts, which could produce very wonderful Effects in changing the Axis of diurnal Rotation, and occasion strange alteration in the Sea's Surface, by Inundation and Recesses thereof, such as History never yet mention'd'. The whole phenomenon is on too large a scale 'and the Places are too far asunder to be influenc'd by the removal of any Magnetical Matter, which may by accident be transplaced within the Bowels, or on the Surface of the Earth'.

This difficulty Halley meets by the bold hypothesis that the earth possesses a core that rotates slightly less rapidly than the outer shell. The shell carries two poles (the fixed magnetic poles of Gilbert) and the core two more. The poles carried by the core move gradually westward relative to the earth's surface owing to the lagging of the rotation of the core behind that of the shell. The elastic and gravitational stability of the system is then briefly discussed and various possible objections mentioned.

It is clear that Halley intended this theory only as a first approximation; he suggests that more than four poles and more than two concentric spheres may be necessary. In a portrait painted when he was 80 years old he holds a diagram taken from his 1692 paper showing three separate concentric spheres within the earth. He estimated the rate of rotation of the core relative to the shell as 0·5° per year, but says 'the nice Determination of this, and of several other Particulars in the Magnetic System is reserv'd for remote Posterity; all that we can hope to do, is to leave behind us Observations that may be confided in, and to propose an Hypothesis which after-Ages may examine, amend or refute.' Modern determinations lie in the range 0·2–0·3° per year.

It is not too much to say that by reading these two papers of Halley's one can learn more about the origin of the earth's magnetic field and its secular variation than will be found in all that was written during the succeeding 250 years. Halley saw the essential points that the widespread anomalies are inconsistent with a local origin and that the time scale of the secular change requires a cause independent of geology, and points to a mobile core. The argument has been carried further in recent years. We now know that the earth has a fluid core and can imagine processes that might maintain electric currents in it, and thus a magnetic field. This gives a greater freedom than Halley's permanently magnetized solid core and allows the foci of the non-dipole field (Halley's extra poles) to wax and wane, as well as moving westward. Halley got as far as he could without electromagnetism, but it is surprising that no one went further for so long.

It is impossible here to discuss every subject that Halley pursued at this period, and the mention of a few must suffice. In 1693 he published a paper entitled 'An Estimate of the Degrees of the Mortality of Mankind, drawn from Curious Tables of Births and Funerals at the City of Breslaw; with an Attempt to ascertain the Price of Annuities of Lives' which gives one of the first attempts to found tables of annuities on a basis of fact. Among his mathematical papers in the Transactions, is one that discusses very clearly some iterative methods for finding the roots of numbers. Such processes have become of importance recently, as they are commonly used in extracting roots by electronic computors; it is surprising to find that Halley was aware of the practical importance of rapid convergence; he knew for instance that if a is an approximate cube root of $(a^3 + b)$ then $a + ab/(3a^3 + b)$ is an approximation in which 'the Figures already found in the Root, would be at least Trebled, which all other ways, are encreased but in an equal number with the given ones'. In another paper he demonstrates that more heat is received from the sun during a summer's day in England than in India. 'A Discourse tending to prove at what time and place, Julius Caesar made his first descent upon Britain' and 'Some Observations and Conjectures concerning the Chinese Characters' are unexpected, but illustrate the width of his interests.

In addition to these investigations he obtained a patent [7, 8] on his improved diving bell in 1691 and promoted a company for using it, the values of whose shares were quoted in the newspapers

during the next few years [7]. From numerous references in the journal book of the Royal Society and elsewhere it is probable that this work took up much of his time.

In 1696 Newton was made Warden of the Mint just as the recoinage of all the old silver coin was starting. This was a large undertaking, and, to maintain a sufficient supply of coin, five mints were opened in provincial towns. Halley was appointed deputy controller of that at Chester, where he remained till 1698 [9].

In 1698 Halley returned to London. His return coincided with the visit of Peter the Great to England. The Czar was aged 26 and had recently obtained control of the Russian government; the main object of his visit was to learn about the building and management of ships. Through this interest he came to know Halley, 'admitted him familiarly to his table, and ranked him among the number of his friends' [3]. The story that he pushed the Czar through Evelyn's holly hedge in a wheelbarrow has, so far as I know, no contemporary authority, though the cost of three lost wheelbarrows and of damage to some holly trees is included among £350 paid by the Office of Works for damage done by the Czar to Evelyn's house and garden [8, 10].

Soon after the Czar left, Halley embarked on the great adventure of his life. He was made captain of the *Paramour*, a naval pink (a small merchant ship), and instructed by the Admiralty to sail to the east coast of South America and the west coast of Africa calling at as many islands as possible, and then 'to stand soe farr into the South, till you discover the Coast of the Terra Incognita, supposed to lye between Magelan's Streights and the Cape of Good Hope'. At all these places he was to determine the magnetic declination and the longitude.

He sailed from Deptford in October 1698, but encountered delays due to leaks and unsuitable ballast in his ship. By February 1699 he got as far as Brazil, but by then it was too late in the season to go far to the southward. On this account, and because of trouble with his officers, he turned homeward, arriving in June 1699. After having his first lieutenant court-martialled and reprimanded for insolence, he set out again in the same ship; this time, after calling at the Cape Verde Islands and at Rio de Janeiro, he reached 52½° S latitude, where, on 1st February, he 'fell in with great Islands of Ice, of Soe Incredible a hight and Magnitude, that I scarce dare write my thoughts of it'. He soon found himself 'in Imminent Danger to looss our ship and lives, being Invironed with Ice on all Sides in a fogg soe thick, that we could not see it till [the ship] was ready to strike against it' [17]. He extricated himself from these dangers and returned home by way of Tristan da Cunha, St Helena, Brazil, the West Indies, and Bermuda, arriving at the end of August 1700.

He brought back 115 observations of the magnetic declination; these and other observations were used to prepare a chart of the Atlantic Ocean showing lines of equal declination. This chart is reproduced in figure 4, being the first map to show the declination (or any other quantity) in this way. For a hundred years such lines were known as Hallean lines. In 1702 Halley produced a similar chart, shown in figure 3, covering the whole world. This chart went through many revisions during the next fifty years and was of great value to navigation. Professor Chapman has given a more detailed account of these charts than is possible here [11].

On these voyages Halley made lunar observations to determine the longitude. He also took with him an ingenious barometer designed by Hooke; in this the air pressure was measured by the difference in the readings of a spirit thermometer and of an unsealed air thermometer [12]. Halley says that the instrument gave reliable warning of storms and was the first barometer successfully used at sea.

The next year Halley was again captain of the *Paramour*. He persuaded the Admiralty to let him spend the whole summer 'Observing the course of the Tides in the Channell of England as well in the mid sea as on both shores' and in taking 'the true barings of the principall head lands on the English Coast one from another, and to continue the Meridian as often as conveniently may be from side to side of the Channell, in order to lay down both coasts truly against one another'. He had a most strenuous summer, anchoring all over the Channel; in a letter to the Secretary of the Admiralty he says 'The frequent weighing my ankers in so deep water has been very hard service to my small company, but the greatest difficulty I find, is from the frequent gales of Wind, which, (especially without the Start) raise the sea to that degree that there is no riding', sentiments which will be shared by anyone who has had occasion to anchor a small sailing ship in deep water in this area. At the conclusion of the work Halley produced a new chart of the Channel.

He spent a large part of 1702 and 1703 visiting Vienna and Istria as a representative of the

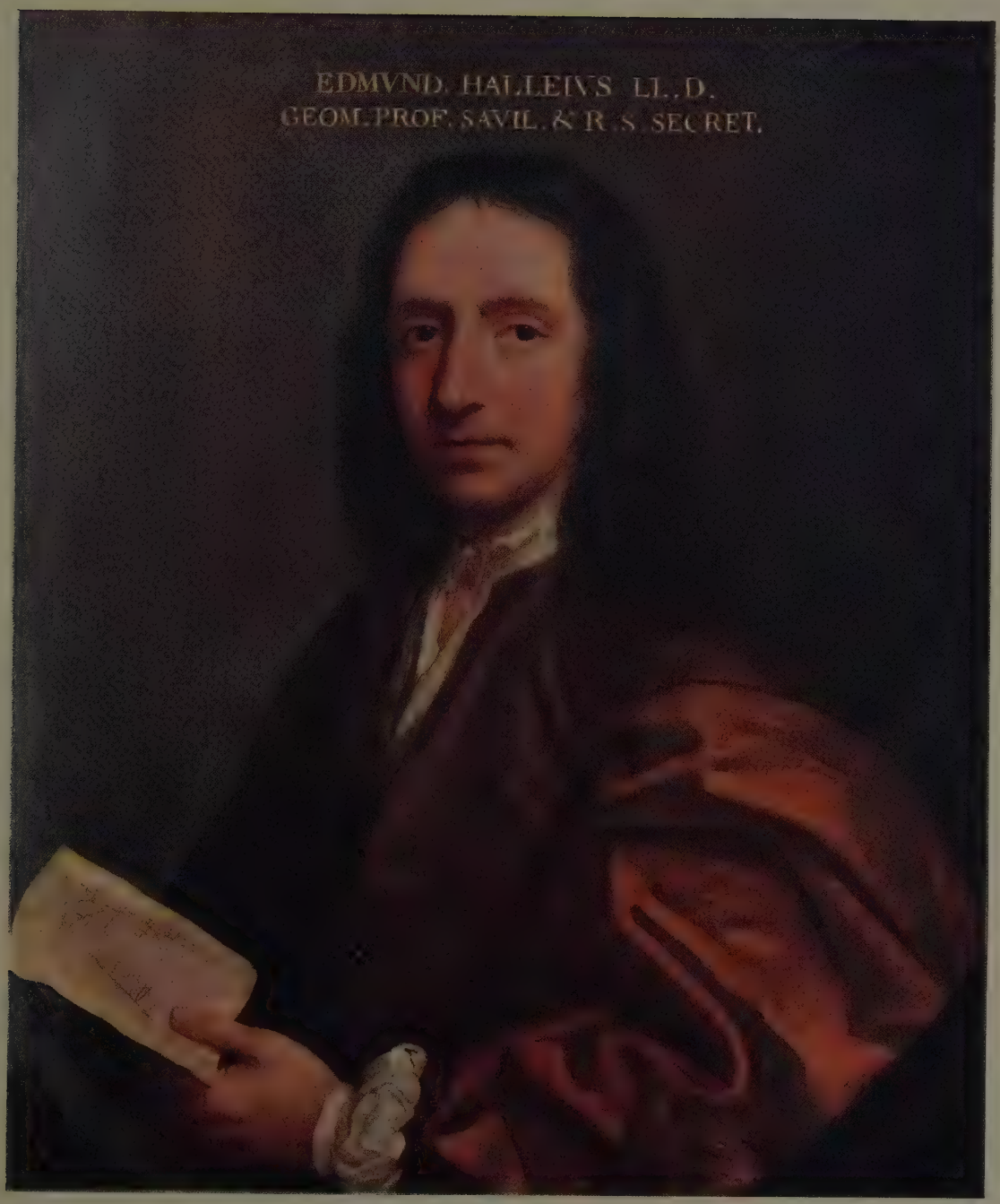


FIGURE 1 – *Halley at the age of about* 30. *This picture is supposed to have been painted by Thomas Murray. Halley holds a diagram representing a geometrical method of determining the roots of a cubic or biquadratic equation by the intersection of a circle and a parabola. The diagram occurs in two papers published in the* Philosophical Transactions *in* 1687. *The picture was probably painted at about that time, that is soon after Halley became Clerk to the Royal Society.* (*Reproduced by permission of the Royal Society.*)

British government, to advise on the fortification of ports on the Adriatic. Halley was now 47 years of age and was one of the best known of the Fellows of the Royal Society, a mathematician, astronomer, and physicist of great distinction, and at the same time a man of the world who 'now talks, swears, and drinks brandy like a sea-captain' [14]. He was not a rich man and had managed to pursue his scientific work only by taking temporary employment first at the Chester mint and then with the Admiralty. Towards the end of 1703 Wallis, the Savilian professor of Geometry at Oxford, died, and Halley was appointed in his place. This was his third attempt to obtain a Savilian professorship. In 1678 Edward Bernard was thinking of resigning his astronomical professorship, and Halley, then a young man of 21 who had not yet taken a degree, was proposed as his successor [15]. In fact Bernard stayed in his professorship till 1691; Halley was then again a candidate, but David Gregory was appointed. It appears that this was due to doubts about Halley's religious views, and in particular to an accusation that he was 'guilty of asserting the eternity of the world'. It is difficult now to judge what Halley's religious views were. They were certainly not strictly orthodox, but I doubt if he was an atheist; he certainly did not believe in the 'eternity of the world', since he saw that this was inconsistent with any friction, however small, opposing the planetary motions. Later he wrote a paper suggesting that the age of the earth might be estimated from the accumulation of salt in the sea, and must, therefore, be finite.

His first undertaking at Oxford was to prepare an edition of the *Sectione Rationis* and the *Conicorum* of Apollonius (he had previously published part of the *Conicorum* in 1700). The greater part of these works was translated from Greek into Latin, but two books of the *Sectione Rationis* and three of the *Conicorum* were known only in Arabic; after a few hints from an Arabic scholar Halley produced a satisfactory translation, including a restitution of some passages in which the Arabic text was corrupt. One book was lost altogether; Halley restored this from a summary given by Pappus and from references to it elsewhere in Apollonius.

In 1705 Halley completed and published his 'Synopsis of the Astronomy of Comets', which he had started about 1695. He collected all the observations of comets that he could find, going back to that of 1337, and deduced the elements of parabolic orbits for 24 of them. The similarity of the elements of the orbit of the comet of 1682 to those found for the comets of 1607 and 1531 suggested to him that these comets were successive returns of a single body whose orbit was not a parabola but a very elongated ellipse, described in about 75 years. Halley predicted the return of this comet in 1758 and suggested that many other comets would prove to move in elliptical orbits. The discovery had been made in 1695, but was not published till 1705. The earlier empirical attempts by Kepler, Hevelius, and the Cassinis to describe the orbits of comets had had very poor success, and the demonstration that they did move in orbits very close to parabolas was a striking verification of Newton's mechanics. The demonstration that 'their Orbits are dispos'd in no manner of Order; nor can they, as the Planets are, be comprehended within a *Zodiak*, but move indifferently every Way, as well retrograde as direct' shows a striking difference from the planets. Halley also pointed out the possibility of a collision between the earth and a comet.

In 1712 Halley published Flamsteed's astronomical observations. This publication was the culmination of a long-drawn-out dispute in which Halley and Newton endeavoured first to persuade and then to coerce Flamsteed into publishing his catalogue of the fixed stars and the places of the moon and planets derived from his observations. The Royal Observatory at Greenwich had been built and Flamsteed appointed 'astronomical observator' by Charles II in 1675. He had a salary of a hundred pounds a year, but was provided with no instruments and no assistant except a 'silly labourer'. His expenses much exceeded his salary, and he not unnaturally regarded his observations as his own property, as did Halley and Bradley after him. He wished to publish his observations as a complete whole in what he regarded as the logical order, first the observations, then star charts, then the catalogue, and finally the positions of the sun, moon, and planets. This plan of observation and computation he pursued with undeviating rigidity for 45 years. The observations were incomparably better than those in the existing catalogues of Tycho Brahe and Hevelius, which were made with plain sights. The results were urgently needed for the practical purposes of navigation and by Newton and Halley for the development of dynamical astronomy.

The clash that ensued was probably unavoidable. It is easy to understand the mounting impatience of Halley and Newton as they saw Flamsteed hoarding a mass of important data while he argued about the proper form of the charts of the

CAROLO II.mo D.G.MAG.BRIT.FRAN.& HIB.REGI SEMPER AUG.
Hanc AUSTRALIS HEMISPHÆRII tabulam
Superis observationibus jussu Regio susceptis, restitutam,
Plurimisq; stellis nondum Globo ascriptis locupletatam,
submisse offert
Subditus Humillimus EDMUNDUS HALLEIUS e Coll: Reg: Oxon.

FIGURE 2 – *Halley's map of the southern stars based on his observations at St Helena. The map includes a new constellation* Robur Carolinum, *named in honour of Charles II. The small diagrams at the top corners show the transit of Mercury observed at St Helena. This is presumably the map Halley gave to Hooke on 31st October 1678 [4] and which Hooke showed to the Royal Society on 7th November. There is a copy in the British Museum bound with Halley's catalogue, but other copies of the catalogue do not contain the map. The author's copy, reproduced here, has never been folded to go in the catalogue; it is therefore probable that it was issued separately.*

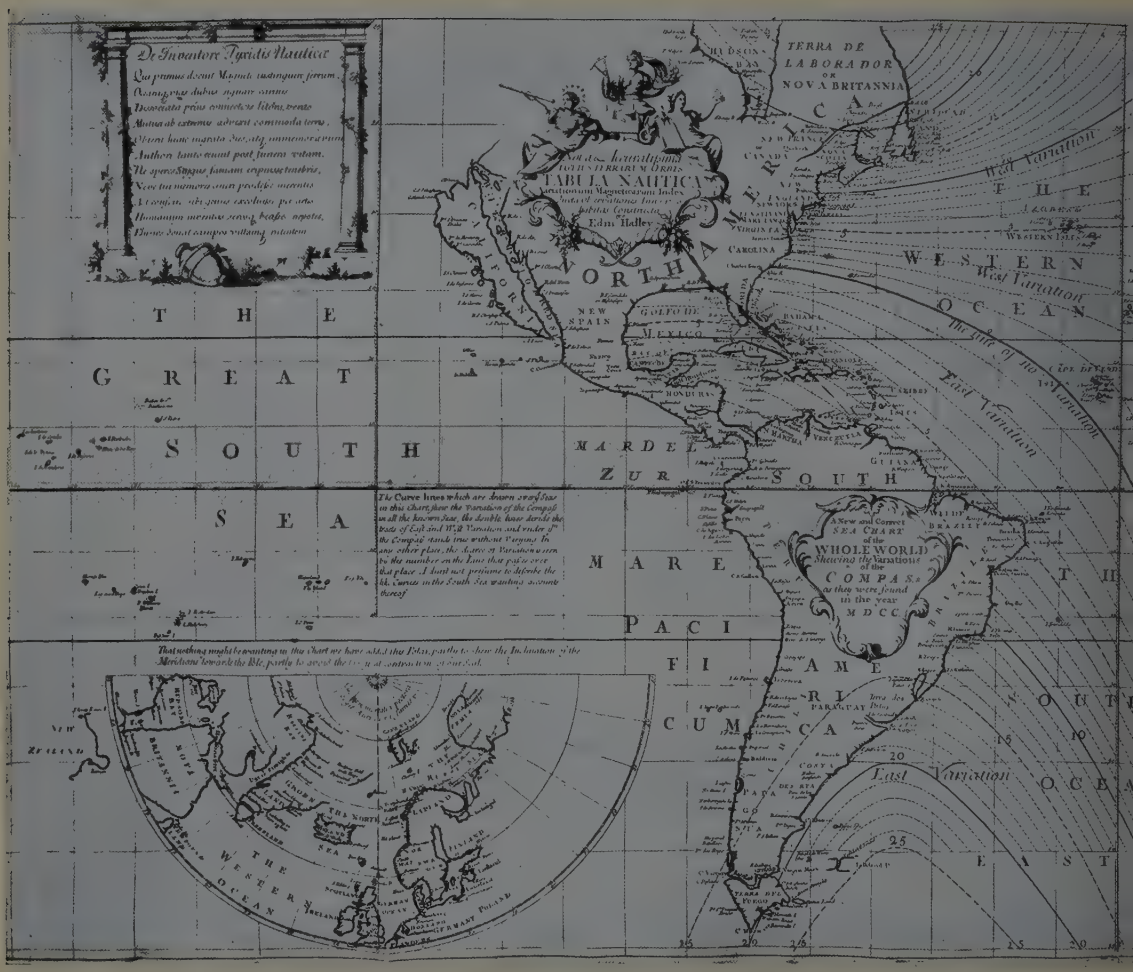
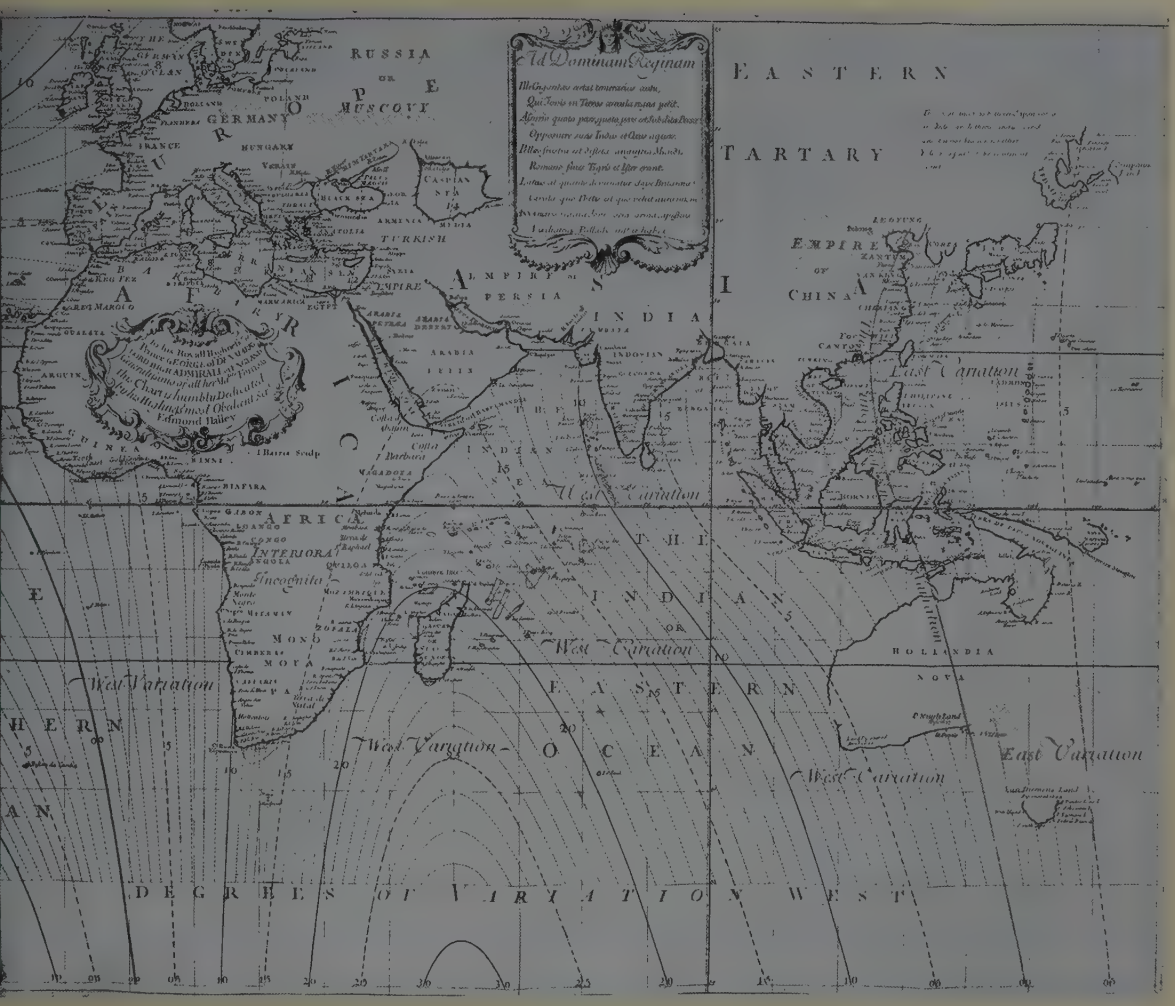

De Inventore Tyridis Nautica
TABULA NAUTICA
Edm Halley
TERRA DE LABORADOR OR NOVA BRITANNIA
THE GREAT SOUTH SEA
MARE PACIFICUM
NORTH AMERICA
SOUTH AMERICA
MEXICO
NEW SPAIN
HUDSONS BAY
CANADA
CAROLINA
WESTERN OCEAN
East Variation
West Variation
A New and Correct SEA CHART of the WHOLE WORLD Shewing the Variations of the COMPASS as they were found in the year MDCC
The Curve lines which are drawn over Sea in this Chart, shew the Variation of the Compass in all the known Sea, the double lines deride the Seas of East and West Variation and under all the Compass stands true without Variation. In any other place, the Curve of Variation were to be the number on the Line that passes over that place. I shall not presume to describe the Sth. Curves in the South Sea standing accounts thereof.
That nothing might be wanting in this Chart we have added the Eclipticque to shew the Inclination of the Meridians towards the Ecl. partly to avoid the confusion of our Sol.
THE WESTERN OCEAN
EAST

FIGURE 3 – *Map of both hemispheres prepared by Halley showing the lines of magnetic declination. Note there*

constellations and the proper Latin names for the joints in the limbs of the mythological figures they were to contain. Flamsteed had come to dislike Halley many years earlier and had been involved in a dispute with him over the tides at Dublin; as the years passed, irritation over the constant pressure to publish his results changed to persecution mania, and in the end no charge was too wild for him to make. Of the Royal Society, with Newton as president and Sloan as secretary, he said ' 'tis governed by persons that either value nothing but their own interests, or understand little but vegetables, and how, by making a bouncing noise, to cover their own ignorance.' He accused Newton of deliberately encouraging the printer to make errors in his catalogue and said that Halley, when helping him 30 years before, had, 'to spoil the Observation, . . . caused me to write *rem*: for *prox*:'. In 1692, in a letter to Newton, he says of Halley 'I have no esteem of a man who has lost his reputation both for skill candor and Ingenuity by silly tricks ingratitude and foolish prate and yet I value not all or any of the shame of him and his Infidel companions being very well satisfied that if χ^t and his Appostles were to walk againe upon earth they should not scape free from ye calumnies



are no magnetic lines over the Pacific. This map, subsequently revised many times, was first published in 1702.

of their venemous tongues, but I hate his ill manners not the man, were he ether honest or but civil there is none in whose company I could rather desire to be' [13, p. 133]. Finally, it became clear that it was impossible to deal with Flamsteed, and Halley published the star catalogue and some other parts of the material in which he and Newton were particularly interested, in the face of Flamsteed's bitter objections.

The detailed history of the affair is a fascinating illustration of the characters of the three main participants: Flamsteed meticulous, always offended, suspicious, and a prig, but also the leading observational astronomer of his age; Newton touchy, often rude, a little inhuman, but really trying to carry out what seemed to him a public duty; Halley, the believer in getting something done, confident that he can reduce Flamsteed's observations better and more quickly than Flamsteed, trying to be tactful and keep on good terms with everyone, but finally exceeding the bounds of prudence and publishing another man's work in the face of his violent opposition. In 1715 Newton's influence with the government was reduced by the death of Halifax, and Flamsteed obtained 300 of the 400 copies of the book printed by Halley.

FIGURE 4 – *Halley's map showing the magnetic declination in the Atlantic Ocean. Published* 1701.

A Description of the Passage of the Shadow of the Moon, over England,
In the Total Eclipse of the SUN, on the 22d Day of April 1715 in the Morning
Firth of Forth
THE GERMAN SEA
SCOTLAND
THE
IRISH SEA
IRELAND
St GEORGE'S CHANNEL
I. Wight
THE CHANNEL
FRANCE

FIGURE 5 – *Halley's map based on observations of the total eclipse of* 1715.

From each copy he extracted 97 sheets containing his observations and burned the rest. These 97 sheets were afterwards used as part of the *Historia Coelestis* published after Flamsteed's death by his widow.

During the next few years Halley published a number of papers, mostly on astronomical topics. The most interesting concerns his collection of observations of the total eclipse of the sun visible at London in 1715. He viewed the eclipse himself from the roof of the rooms of the Royal Society and describes the corona and prominences. His map based on the observations is reproduced in figure 5.

In 1720 Flamsteed died, and Halley succeeded him as Astronomer Royal. He found the observatory stripped of all instruments by Flamsteed's executors, and it was some time before he could start effective observation. He then, at the age of 65, embarked on the project he had formed 40 years before, to observe the moon through the 18-year period of the Saros. In this he succeeded, though the work was not in all respects satisfactory [16], and he has the dubious distinction of being the only Astronomer Royal whose observations it has not been thought necessary to publish. His astronomical tables were published posthumously in Latin in 1749 and were reprinted several times in English and French.

Towards the end of his long life Halley became a little infirm, probably as the result of a stroke. He also lost all his teeth and lived largely on fish. He had, however, 'a vein of good humour, which neither his abstracted speculations, the infirmities of old age, nor the palsey itself, which seized him some years before his death, could impair: and this happy disposition, the gift of nature, was the more perfect, as it was still attendant upon that peace of mind, which is the nobler endowment of virtue' [3]. He died, still Savilian Professor of Geometry, Astronomer Royal, and a Naval Captain on half pay, at the age of 85 in 1742.

Looking back at Halley's multifarious activities and achievements, it is perhaps as a collector and organizer of data that his genius is most apparent. Again and again he collects a mass of information of varying reliability, containing many errors and contradictions, and reduces it to order. He did this with the magnetic observations, with the tides in the Channel, with the comets, with the eclipse of 1715, and with the moon's orbit. His remarkable work on the path of the great meteor of 1719 is of the same kind, and so is his discussion of the trade winds. He was often a rash speculator and we now know that he was sometimes wrong in his conclusions. He had, however, a very sound instinct for physics; in mathematics, his work was outstanding. Some of the things he was most interested in have again become fashionable subjects of study only in our own day; Halley therefore appears to us not as a mere follower of Newton, but as the fountain head of many of our own interests. That he was also the first man who borrowed a ship from the Admiralty for an expedition with a scientific purpose, and the man who persuaded the government to pay for the instruments at Greenwich Observatory, increases our gratitude to him and our respect for his powers.

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The dynamics of the pneumatic tyre

G. TEMPLE

While there is abundant literature on the technological and engineering aspects of the pneumatic tyre, there appears to have been relatively little treatment by the physicist and applied mathematician. The mechanical behaviour of the tyre is here examined in terms of its reaction to the various forces arising during manœuvring of the wheel and the vehicle. Although results of much interest have been obtained, the complex structure and behaviour of the tyre have so far precluded the establishment of a complete and satisfactory theory.

The dictionary describes the pneumatic tyre as an endless air-cushion fitted to the rim of a wheel in order to improve its riding qualities. This description does scant justice, however, to a major invention in transport, worthy to take its place with the ice-skate and snowshoe and almost as great a triumph of engineering as that pre-eminent discovery—the wheel. This article will focus attention on the essential properties of the pneumatic tyre as a medium for the transmission or suppression of forces between the wheel and the ground. The pneumatic tyre will be called here simply the tyre, the other species of this genus being distinguished as solid tyres.

The behaviour of the tyre can be most strange, and even the light cast by Newtonian dynamics is scarcely adequate to elucidate all its mysteries. Even today the tyre is full of surprises and still provides a rich field for research. Just as all the problems of structural engineering are found in their most acute and intractable form in aeroplane construction, so all the problems of tyres are accentuated to the utmost when they are fitted to the wheels of aircraft. Considerable impetus has been given to tyre research by problems posed by the landing-run, taxying, steering, and braking of aircraft wheels, and the most valuable available compendium of information on the mechanical characteristics of tyres was issued as an Aeronautical Research Council Report [1].

CLASSIFICATION OF PROBLEMS

From the point of view of the natural philosopher, if not from that of the engineer, the mechanical behaviour of the tyre is conveniently and systematically studied in terms of its reactions to the various kinds of forces which are elicited during different manœuvres of the wheel and of the vehicle to which it is fitted.

First, the tyre is called upon to support the vertical axle load, either as a steady load, while the vehicle is at rest or running over the ground, or as a variable load, as when an aircraft is landing on a runway.

Secondly, the tyre is the medium for the transmission of the fore and aft horizontal forces which are effective in driving or braking the wheel.

Thirdly, the tyre is invoked to supply the sideways horizontal forces which are required in steering.

The manœuvres just listed may all be described as natural, but there are also certain artificial manœuvres employed in testing tyres which require examination—the types of static deformation used in tests of tyre elasticity, the steady rolling motion in the 'crab walk,' the self-aligning property, and last, but not least important, the oscillatory motion known as shimmy or wobble.

The complexity of the structure and behaviour of the tyre are such that no complete and satisfactory theory has yet been propounded. The characteristics of the tyre still present a challenge to the natural philosopher to devise a theory which shall co-ordinate the vast mass of empirical data and give some guidance to the manufacturer and user. This is an inviting field for the application of that method of idealization which is a standard technique in the application of mathematics to the physical world.

IMPORTANCE OF GROUND REACTIONS

Consider a wheeled vehicle accelerating on a level road. What is the cause of this motion? For the magistrate it is the driver in charge of the vehicle; for the engineer it is the engine which provides the propulsive power; but for the applied mathematician it is the forward thrust exerted by the road on the wheels or tyres. For the layman this is a difficult conception, but it is an inescapable conclusion from Newton's first law of motion. According to this, only external forces are effective in producing acceleration, and (on the level) the

only external forces are provided by the road and the resistance of the air. The same conclusion follows if the vehicle is being retarded or steered round a corner. It is the reaction between the tyres and the ground which provides the necessary force. Hence the prime subject of our study must be the reactions between the tyre and the ground.

When we study the wheel and tyre as a closed dynamical system we must also include the forces transmitted to the wheel through the axle, the driving couple, braking force, the steering force applied to the wheel, and the adhesion between the tyre cover and the rim of the wheel. These forces determine the motion of the wheel and tyre, and the ultimate goal of our investigation is to determine the response of the wheel and tyre to these forces in terms of the measurable characteristics of the tyre.

It is a sobering thought that all the forces required to drive, brake, or steer the car are transmitted through the tyre—a channel-shaped envelope of rubber, strengthened with a warp and woof of cord threads and by the bead wires along the edges of the tyre cover, and deriving almost all its rigidity from the air pressure in the inflated inner tube.

VERTICAL LOADS AND FREE ROLLING

The stress system in a free inflated tyre—as observed, for example, when the axle is jacked up until the tyre is clear of the ground—is comparatively simple. The air pressure is resisted by circumferential and transverse (hoop) stresses in the cover, and by a longitudinal tension in the bead (figure 1), which presses uniformly on the rim of the wheel. But when the jack is removed and the load of the vehicle begins to press on the axle the situation is much more complex, even when we neglect the effects of camber and 'toe-in'.

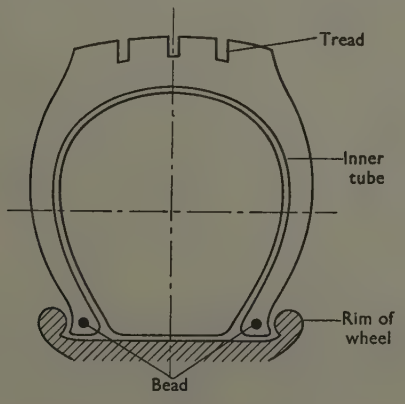

FIGURE 1 – *Cross-section of tyre.*

The tyre becomes squashed by the upward pressure of the ground, and the load carried by the wheel is roughly equal to the product of the inflation pressure—by which is meant the gauge pressure, i.e., the excess over atmospheric pressure as indicated in the standard tyre pressure gauge—and the area of the contact region. But, of course, the load is not transmitted by the air, but by stresses in the tyre cover. In fact the tyre cover functions in the same way as the tensioned spokes of a bicycle wheel, which support the axle by reason of the increased tension in the spokes above the axle, and the reduced tension in the spokes below. Similarly the axle of a car hangs in the tyre (figure 2), being carried by the difference between the increased transverse tensions above and the reduced transverse tensions below.

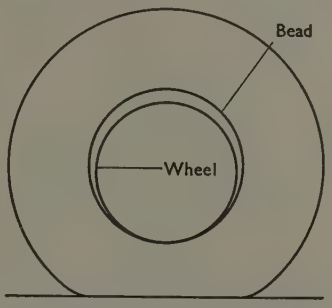

FIGURE 2 – *Illustrating how the wheel load is carried by the tyre.*

The first great advantage of the pneumatic tyre as compared with the solid tyre is that the squashing and distortion of the tyre distributes the load over a much greater contact area, and therefore enables a vehicle to move over fairly soft ground into which a rigid wheel would sink axle-deep. Low-pressure tyres invite comparison with the padded soles on the feet of a camel, which expand when the camel is fully loaded and reduce the contact pressure to about seventeen pounds per square inch. High-pressure tyres, such as are used on many civil aircraft, may have an inflation pressure of 100 pounds per square inch, and of course they can be used only on hard runways with a good thickness of concrete on a stabilized subsoil.

The great advantage of the wheel is the lower resistance which it elicits from the ground when freely rolling, and this advantage is retained when the wheel is fitted with a pneumatic tyre. The rolling resistance, i.e. the ratio of the horizontal

drag D to the vertical load W, varies with the forward speed, the softness of the ground, and the type of tyre. At lower speeds on hard roads a representative figure for the rolling resistance is 20 pounds per ton, or 1 per cent.

The horizontal drag has a moment about the axle and therefore tends to give angular acceleration to the wheel. To balance this effect the vertical reaction of the ground must move forward a distance x from the centre of the contact region and produce a decelerating moment about the axle such that $Wx = Dh$, where h is the height of the axle above the ground (figure 3). This movement of the centre of pressure is doubtless associated with the adoption of an unsymmetrical shape by the rolling tyre.

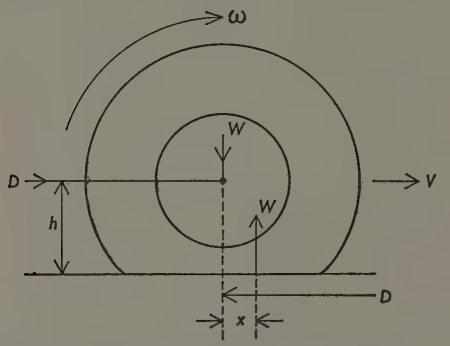

FIGURE 3 – *Forces acting during free rolling with uniform forward velocity* V.

The third attractive characteristic of the tyre is the 'cushioning' effect which it produces when rolling over obstacles and uneven ground. The way in which this effect is produced is that obstacles are, as it were, swallowed by the tyre, which distorts in such a way that the axle continues to move horizontally as the wheel rolls over the obstacle. The extraordinary efficiency of this process can be appreciated by estimating the vertical acceleration produced when a rigid wheel of radius R rolls with speed V over an obstacle of height h (figures 4(*a*) and 4(*b*)). The maximum vertical velocity and acceleration are easily proved to have values exceeding hV/d and $2hV^2/d^2$ respectively, where $d = (2Rh - h^2)^{\frac{1}{2}}$ is the distance through which the wheel moves forward as it rises over the obstacle. The maximum vertical acceleration therefore exceeds V^2/R. In a wheel of 3 feet diameter, moving at 30 miles per hour, this gives the fantastic figure of 15 times the acceleration due to gravity.

To complete this rapid summary of the action

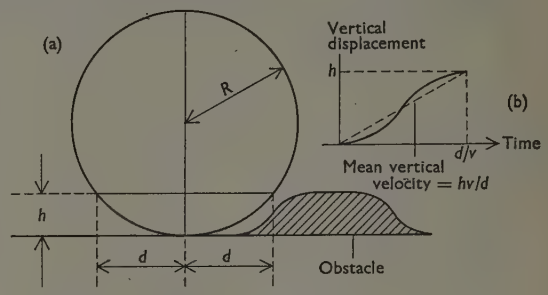

FIGURE 4 – *Rigid wheel riding over an obstacle.*

of the tyre in sustaining vertical loads, reference must also be made to the function of aircraft tyres as shock absorbers in the touchdown. Here the tyres co-operate with the hydraulic shock absorbers in the main undercarriages in absorbing the kinetic energy of the vertical component of the velocity of the aircraft on landing.

A curious and interesting feature of the rolling motion of a tyre is the relation between the effective rolling radius r and the height of the axle above the ground (figure 5). The rolling radius is

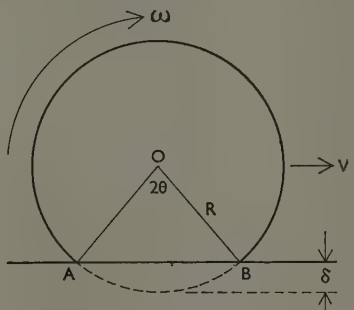

FIGURE 5 – *Rolling radius of tyre.*

defined as the ratio of the forward linear speed V of the axle to the angular velocity of the wheel ω. Experiments show that at low speeds the rolling radius is less than the radius R of the free, inflated, and undeflected tyre by about one-third of the tyre deflection δ. This can be deduced theoretically as follows: Let $2l$ = chord $AB = 2R \sin\theta$ in figure 5, and arc $AB = 2R\theta$. Now $2\theta/\omega = 2R \sin\theta/V$, and $\delta = R(1 - \cos\theta) \simeq \frac{1}{2}R\theta^2$. We therefore have for the rolling radius

$$r = V/\omega = R \sin\theta/\theta \simeq R(1 - \tfrac{1}{6}\theta^2) = R - \tfrac{1}{3}\delta.$$

This is probably the explanation of the known fact that the accuracy of speedometer readings is insensitive to variations in tyre pressure and deflection.

The compressive strain on the tyre is given by

$2R(\theta - \sin\theta)/2R\theta \simeq \frac{1}{6}\theta^2 = \frac{1}{3}\delta/R$, that is, one-third of the ratio of the tyre deflection to its undeflected radius. This calculation is confirmed by experiment.

HORIZONTAL FORCES AND BRAKING

The stress system in the tyre cover when a driving torque or a braking torque is applied to the wheel is highly complex, but there are simple approximate expressions for the empirical values of the ground reaction which is elicited. There are few facts available for the driven wheel but abundant information on the effect of braking.

The maximum braking effect is limited by three conditions—the adherence of the tyre to the wheel, where the bead presses against the rim; the maximum shear stress which the cover can carry without tearing; and the adherence of the tyre to the ground. It is the last condition which is most important. Its effect is to limit the retarding force, which acts in the contact region, to the product of the vertical load by the coefficient of ground friction. This coefficient of friction can vary over a wide range, from 1·0 for treaded tyres on dry ribbed concrete to 0·1 or less for smooth tyres on an icy runway.

The maximum ground friction is obtained when there is skidding over the whole of the contact area. This condition always occurs when an aircraft touches down and the wheels, which are initially non-rotating, are spun round by ground friction. During this process, which occupies about a tenth of a second, a thin surface layer of the rubber of the tyre cover is melted by the heat generated, there is a puff of smoke from the burning rubber, a characteristic squeal, and a black mark of melted rubber left on the runway. Surprisingly enough the tyre wear produced is negligible, and pre-rotation of the wheels before landing is as unnecessary as it would be difficult.

It is perhaps even more interesting to study the régime of moderate braking. Its effects are conveniently measured by the wheel slip, i.e. by the percentage reduction in the angular velocity from the value appropriate to pure rolling. The application of the brake imposes a tensile stress on the tyre, with the result that the tyre has an initial tensile strain before it enters the contact area. This increases the effective rolling radius, and the effect persists until the slip is numerically equal to the compressive strain in the contact area of the freely rolling tyre.

Under these conditions limiting friction will first occur at the rear of the contact area and will extend forward as the braking effect is increased. The total frictional drag on the contact area is proportional to the slip until the condition of limiting friction is attained all over the contact area. Thereafter the frictional drag is roughly constant and equal to the maximum value quoted above (figure 6).

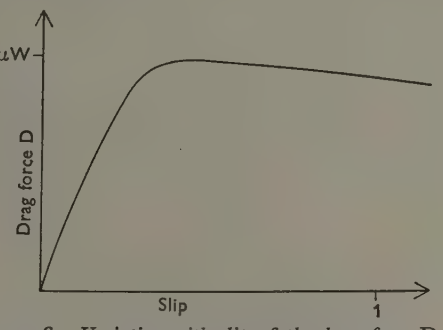

FIGURE 6 – *Variation with slip of the drag force* D *on a braked wheel.* (W = *wheel load,* μ = *coefficient of friction.*)

SIDE FORCES AND CORNERING

The nature of the sideways horizontal forces exerted by the ground on the tyre during cornering and similar manœuvres is best appreciated in the light of a qualitative theory of tyre characteristics. In this theory attention is concentrated on the central line which runs round the periphery of the tyre cover. This equatorial line is sometimes called the tread line. The problem is then restricted to a consideration of small lateral displacements of this line from its normal position in the free and undeflected tyres. In order to obtain a simple representation of the elastic characteristics of the tyre it is assumed that the tread line behaves like a stretched string restrained by a continuously distributed restoring force proportional to its displacement. Its elastic behaviour will then be specified by two parameters—the restoring force per unit length per unit lateral displacement K, and the equivalent tension in the tread line, which is conveniently written as $K\sigma^2$, where σ has the dimensions of a length. The problem is then to express all the lateral elastic properties of the tyre in terms of these two parameters K and σ.

It may very well be that it is necessary to introduce as a third parameter the effective flexural rigidity of the tread line and to think of this line as resisting sideways deformation not only as a spring and as a stretched string, but also as a beam. The consequences of this assumption have not been worked out in any detail.

The two fundamental measurements of tyre characteristics determine the lateral and torsional elasticity of the loaded tyre as it stands or rests on the ground. The wheel and tyre are maintained in a vertical plane by suitable fixing couples. To measure the lateral elasticity, a horizontal side force F is applied at the axle, while an equal and opposite force is provided by ground reactions, which hold the contact region fixed. The sideways movement of the wheel, a, is found to be proportional to the side force F, and the ratio $N = F/a$ is the lateral elasticity. In this test the lower part of the tyre is deflected sideways as the wheel moves relatively to the fixed contact region (figure 7).

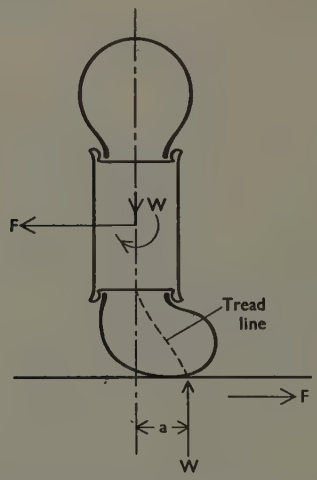

FIGURE 7 – *Illustrates the principle of the measurement of lateral elasticity, the ratio of the side force* F *to the wheel sideways movement* a.

To measure the torsional elasticity, a torque T about a vertical axis is applied to the wheel, an equal and opposite torque being provided by ground reactions. The angular rotation of the wheel, α, about the vertical axis is proportional to the torque T, and the ratio $S = T/\alpha$ is the flexural elasticity.

It is not difficult to carry out these tests for automobile tyres, but it is a major operation to do so for aircraft tyres because of their size and the heavy loads which have to be applied. The numerical values obtained for the lateral and torsional elasticity vary considerably with the different types of tyre [1]. The theoretical values, which depend only on the parameters K and σ and the semi-length l of the contact region, are

$$N = 2K(\sigma + l)$$

and

$$S = 2Kl[\tfrac{1}{3}l^2 + \sigma(\sigma + l)].$$

The automobile engineer is interested not so much in these fundamental elastic constants as in the behaviour of the tyre as the vehicle is steered round a corner. In this manœuvre the tyre executes a kind of 'crab walk', the plane of the wheel being inclined at an angle of yaw θ to the direction of motion of its centre. The elements of the tyre in the contact area adhere to the ground, so that in the contact area the tread line remains parallel to the direction of motion of the centre of the wheel, and the contact area is deflected sideways. As a result a side force F acts on the tyre in the contact region at a distance c behind the vertical through the centre of the wheel (figures 8 and 9).

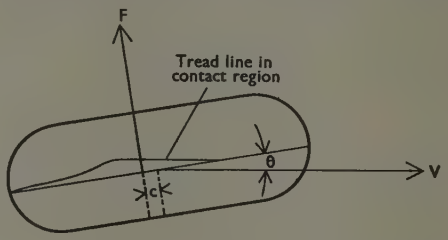

FIGURE 8 – *Side force* F *in 'crab walk' at a cornering angle* θ.

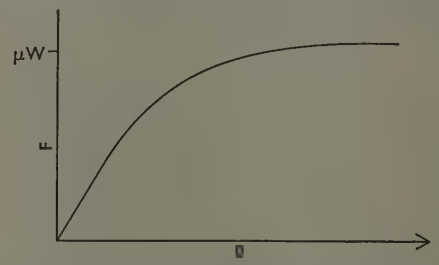

FIGURE 9 – *Variation of side force* F *with the angle of yaw* θ *during cornering.*

The cornering power F/θ is given theoretically (for small values of θ) as

$$F/\theta = 2K(\sigma + l)^2$$

and the pneumatic castor, c, as

$$c = l[\tfrac{1}{3}l^2 + \sigma l + \sigma^2]/(\sigma + l)^2.$$

It is the cornering force F which provides the external force necessary to give the vehicle the sideways acceleration corresponding to a turn with speed V in a turning circle of radius r. In order to study the characteristics of a car during steering it is, of course, necessary to consider the cornering forces on all four wheels, together with the rolling of the chassis on the springs.

There is another type of motion of the wheel and tyre which is extremely curious and interesting for the information which it can give about the

tyre parameter σ. In this type of motion the initial configuration is the same as for the measurement of the lateral elasticity, i.e. á suitable side force and couple are applied to the loaded wheel so as to compel it to move sideways while the contact area of the tyre is held fixed by adhesion to the ground. The wheel is then compelled to move forward in its own vertical plane. It is then found that the contact region of the tyre gradually moves sideways (as well as forward) until it is under the centre of the wheel. The track of the tread line on the ground is a die-away exponential curve, with an equation of the form

$$g = g_0 \exp(-x/\sigma),$$

so that its sub-tangent is of constant length, exactly equal to the tyre parameter σ, and is therefore appropriately called the relaxation length. This curious effect, first discovered by Kantrowitz, is easily incorporated into the elementary theory of the tread line described above. The direct measurement of the relaxation length (usually comparable with the tyre radius) is obviously of great value in providing a value of σ, which can be used to check the theoretical values of the lateral and torsional elasticity.

WHEEL WOBBLE OR SHIMMY

The pneumatic tyre also has the power of developing spontaneous oscillations in which the wheel swings to and fro about a vertical diameter. This type of instability usually occurs only at high speeds, and it is well known to racing motor-cyclists and car drivers. The literature of the subject is extensive, and the technical language extremely expressive.

Automobile engineers speak of this type of wheel vibration as wheel wobble or shimmy, and they regard it as one of the many kinds of wheel fight with which the driver has to contend. In the case of cars it is thought to be produced by a coupling between wheel flap and car shake, i.e. between the oscillation of the wheels about the king-pins and a rolling or yawing oscillation of the car body. In the case of aircraft the oscillation of the fuselage seems to be of small importance, and the main factor is the interaction of wheel oscillation with tyre distortion.

The simplest way of regarding shimmy in aircraft wheels is to emphasize the difference between the side forces acting on the tyre under steady conditions, when the wheel makes a fixed angle with its direction of advance, and during oscillation, when the wheel is swinging to and fro. In the second case the side force is no longer in phase with the angular displacement of the wheel, but lags behind. This is largely due to the fact that changes in the position of the contact region are not instantaneous, but are effected by new elements of rubber entering the front of the contact region. These changes are then propagated through the contact region with the same speed as the speed of advance of the wheel.

It is well known that a lag in the restoring force of a spring is roughly equivalent to the addition of negative damping, which naturally produces a divergent oscillation. When the amplitude of the oscillation becomes so large that the tyre skids at the end of each swing, a régime of steady oscillation is produced. The vehicle becomes uncontrollable, and structural damage may be produced by the violence of the vibrations. The simplest cure is to introduce sufficient torsional damping into the wheel suspension or tyre to suppress shimmy, but not too much to make steering and castoring difficult.

Shimmy in pneumatic-tyred wheels can be compared with the more familiar wheel wobble in the solid-tyred wheels of luggage trucks and the domestic tea trolley. In these vehicles shimmy is usually associated with a fair amount of slack in the mounting of the wheels on their axles. This slack allows the wheel to slide sideways on its axle and introduces a certain lag in the development of the side force on the wheel due to ground friction. Small oscillations can therefore grow into persistent oscillations, with an amplitude controlled by the amount of slack on the wheel axle.

A large number of factors control the development of shimmy, and a complete theory is elaborate and complex.

CONCLUSION

This article does little more than summarize the bald facts concerning the dynamics of the pneumatic tyre, but even so it will be apparent that this is a subject not only of immediate practical interest to the car driver and aircraft pilot, but also a topic of considerable intrinsic interest to the applied mathematician.

For further information on the subject the reader is referred to the report by Hadekel [1], to the publications of the Road Research Laboratory of the Department of Scientific and Industrial Research, and of the Society of Automotive Engineers.

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The bubble chamber

C. DODD

Modern machines can provide pulses of high-energy particles at intervals of a few seconds, which is considerably more rapidly than the detecting devices hitherto in use can be operated. An important feature of the newly developed bubble-chamber detectors is that they can keep pace with the new particle accelerators. They possess the further important features that they have no background of irrelevant tracks and that, because of the high density of the medium, there is a relatively high probability of a collision being recorded.

Progress in high-energy nuclear physics depends largely on the availability of suitable particle detectors, in particular of those giving a photographic record of the paths of high-energy particles and of the fragments resulting from their collisions with other nuclei. The Wilson cloud chamber, using a gaseous medium, and the photographic emulsion, using a solid medium, are now well known examples of this kind of detector. It is perhaps not surprising that when changing circumstances emphasized the deficiencies of both these media, physicists should have considered the possibilities of a liquid medium. Circumstances calling for a new type of detector arose from the discovery of two groups of particles, the hyperons and κ-mesons [1] in cosmic ray experiments. The rarity of the natural production of these particles stimulated the design of accelerating machines of much greater energy than before, capable of producing the particles in copious quantities for investigation. It became apparent that, apart from other considerations, neither of the existing types of detector was able to keep pace with the increased output of such machines and that a detector using a liquid medium was more suitable.

The cloud chamber utilizes the fact that condensation of a liquid can occur on ions produced in a gas which has just undergone an adiabatic expansion. The line of liquid drops is photographed as soon as these are large enough, but during the period of growth the original line of drops may be distorted by the swirling produced in the gas by the expansion process: consequently the trace recorded on the photograph is not a faithful representation of the particle track. The density of the gas is low compared with that of a solid or liquid and the probability of an incoming particle making a collision and producing one of these new particles is very small; moreover about ten seconds must elapse before the gas can be re-expanded ready for the next picture. The probability of producing a collision in the chamber can be increased by inserting lead plates in it, but the length of the track then becomes indeterminate and details of the collision are hidden in the plates. A solution to the problem is to increase the density of the gas by raising its pressure to about 100 atmospheres, but this unfortunately increases the cycling time to about 15 minutes. Since modern machines are capable of providing a pulse of particles every few seconds the cloud chamber is unable to take full advantage of their output, which is achieved only with very heavy expenditure. The high-pressure diffusion cloud chamber is continuously sensitive, but the extent of the layer in which tracks can be made visible is too small to reveal all the details of a three-dimensional collision process.

In the photographic emulsion the medium is of sufficient density to ensure a high probability of production of nuclear collisions, but as the plates are sensitive to stray radiation from the time of their manufacture until they are developed, the background of unwanted tracks makes it almost impossible to sort out with certainty events which are associated with each other. Moreover, deflections are imposed on each track as a result of multiple scattering of the particle by the heavy atoms comprising the emulsion: consequently the effect of a magnetic field cannot be used, as it is in the cloud chamber, to determine the momentum of the particle. The tracks formed in emulsions are so short that a microscope must be used to locate and follow them, making the analysis extremely slow.

The bubble chamber depends for its action on the fact that when the external pressure on a liquid is suddenly reduced to a value much less than the saturation vapour pressure of the liquid at the prevailing temperature, boiling does not begin until a finite time has elapsed. During this time the liquid is superheated and in a state of unstable equilibrium which when upset results in

the violent formation and growth of bubbles known as 'bumping'. This delay before the onset of boiling is due to the fact that surface tension forces acting on a microscopic bubble in the liquid tend to collapse the bubble, while the internal vapour pressure tends to expand it. The effect of surface tension decreases as the size of the bubble increases: if the bubble exceeds a certain size the net effect is one of expansion, which causes the bubble to grow and reach visible size extremely quickly. The delay thus represents the time required for random thermal fluctuations to produce in the liquid a bubble large enough for such growth to be possible. When the liquid is contained in a smooth vessel this delay can be several seconds [2].

It was discovered by D. A. Glaser [3] in 1952 that an ionizing particle passing through a sufficiently superheated liquid immediately upset the unstable equilibrium and initiated boiling at points in the liquid lying along its path; by high-speed photography he was able to trace the rate of growth of the string of bubbles marking the track of the ionizing particle. The particle produces charged ions in the liquid along its path: presumably this electrical energy reappears as thermal energy which raises the temperature of the liquid in the region of this path. As a result the surface tension tending to collapse any minute bubble in the neighbourhood is decreased and at the same time the internal vapour pressure increases, so that even the most minute bubble formed spontaneously grows in size indefinitely.

If the vessel containing the liquid is made of metal with flat glass observation windows, boiling always begins at the junctions of the metal and glass as soon as the external pressure on the liquid is reduced. If, however, this pressure reduction is carried out very rapidly, the pressure in the liquid away from the walls attains a low value which is maintained for about a hundredth of a second. During this time the liquid is in a superheated state which is immediately upset by the passage of an ionizing particle [4].

Most bubble chambers are now of this type and consist essentially of a thick-walled metal container having two plane glass windows and containing the liquid, which is maintained at a constant temperature considerably above its normal boiling point (figure 2). Pressure sufficient to prevent boiling is applied by compressed air acting on a piston or flexible diaphragm in contact with the liquid. To render the chamber sensitive the compressed air is allowed to escape through a quick-acting valve. The beam of ionizing particles from the accelerator is then pulsed to traverse the chamber, and a few thousandths of a second later, during which time the individual bubbles along the track have grown to a diameter of about 30 μ, an intense flash of short duration is triggered off so that the track can be photographed. The chamber can be recompressed and ready for the next expansion within a few seconds, or even within a fraction of a second: consequently it is possible to use every pulse from the accelerator and to obtain many thousands of pictures in a single day. A substantial fraction of these pictures can be expected to be of use in the study of nuclear collisions and new particle production, for the probability of the incoming particle making a collision is high because of the relatively high density of the liquid medium. Indeed, a bubble chamber only 10 cm long is able to yield as many collision events as a cloud chamber over 40 m long.

Moreover, the tracks formed in a bubble chamber do not suffer from the distortion, due to motion of the medium, which occurs in a cloud chamber, for the photograph is taken only a few milliseconds after the formation of the bubbles and the inertia of the liquid is such that its motion in such a short time is negligible. Another major advantage of the bubble chamber—freedom from a background of unwanted tracks—arises from the fact that the chamber can record tracks only during the brief time, less than a hundredth of a second, that the liquid is in the superheated state. The interpretation of a complicated event on a bubble chamber photograph is thus a much more certain process than it is in a photographic emulsion.

The velocity of a particle can be deduced from the number of bubbles formed per unit length of its track—a procedure similar to droplet counting in cloud chambers and grain counting in emulsions.

Up to the present, every liquid which has been tried has proved to be suitable for use in the bubble chamber, but since the mechanical construction of a chamber strong enough to withstand pressures much in excess of 30 atmospheres is difficult, liquids requiring high operating pressures are to be avoided. Since the operating pressure is roughly two-thirds of the critical pressure, this means that liquids with a high critical pressure, such as water, are unsuitable. Propane, xenon, and hydrogen are the chief liquids in current use. Liquid hydrogen is undoubtedly the ideal medium, since its nuclei are all protons: the collision processes resulting from its bombardment by other

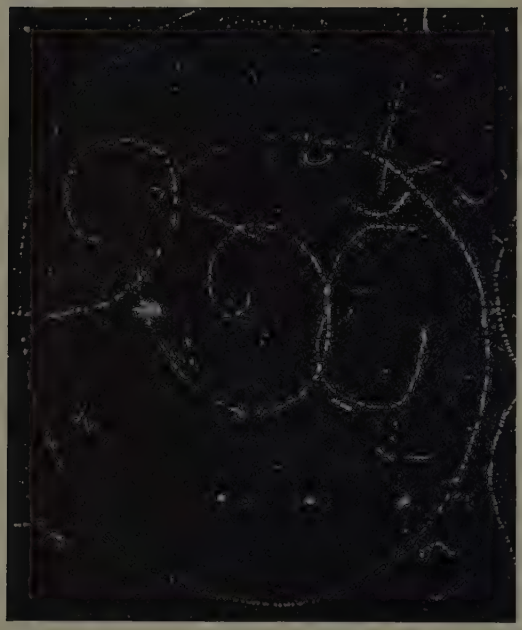

FIGURE 1 – *Photograph of electron tracks taken in a liquid-hydrogen bubble chamber. The electrons are made to follow anti-clockwise spiral paths by a strong applied magnetic field, the imposed curvature increasing as the electron is slowed down by the liquid. (Photograph reproduced by kind permission of Professor Luis Alvarez.)*

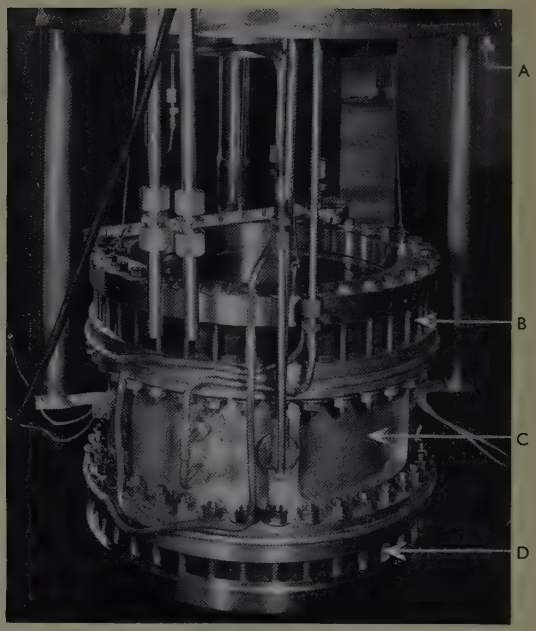

FIGURE 2 – *The liquid-hydrogen bubble chamber of the Radiation Laboratory, California. The sensitive volume is a cylinder of diameter 25 cm and depth 15 cm; the glass windows are 5 cm thick. In operation the chamber must be placed inside an evacuated tank. A, liquid-hydrogen bath; B and D, glass windows; C, stainless steel chamber containing liquid hydrogen. (Photograph reproduced by kind permission of Professor Luis Alvarez.)*

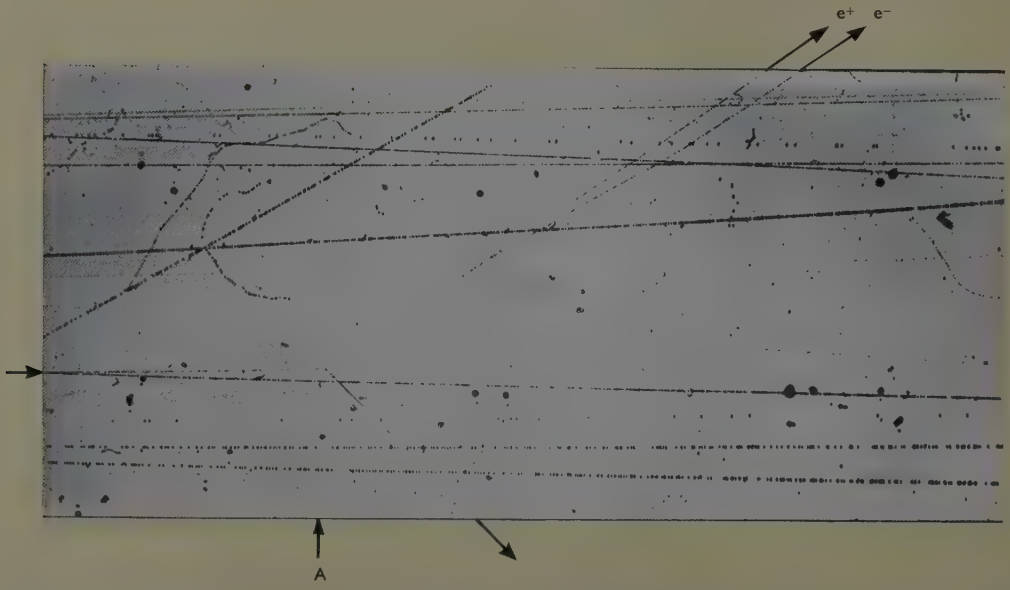

FIGURE 3 – *A typical photograph obtained in a liquid-propane bubble chamber exposed to the 2 GeV beam from the Brookhaven Cosmotron. The beam enters from the left and most particles traverse the chamber, which is 15 cm long, without making a collision. At A an incoming π-meson collides with a proton, producing a γ-ray which leaves no track but whose direction is determined from the tracks of the pair of oppositely charged electrons which it produces. (Photograph reproduced by kind permission of Professor D. A. Glaser.)*

particles produced by machines can thus be more unambiguously interpreted than collisions occurring in any other liquid. The experimental difficulties are, however, very great, since the operating temperature is about 27° A and the pressure about 6 atmospheres. Nevertheless a chamber of diameter 25 cm and depth 15 cm has been operating successfully for some time at the University of California in the 6·3 GeV beam from the Bevatron and in a strong magnetic field which enables particle momenta to be deduced from the curvature which the field imposes on the tracks (figure 1).

In laboratories where a sufficient supply of liquid hydrogen is not available the medium is usually liquid propane, chosen because of its cheapness, its convenient operating temperature (about 60° C), and the fact that it contains only two relatively light atoms, carbon and hydrogen (figure 3). Xenon is attractive as a bubble chamber liquid because its density (about 2·3 g/cm^3) approaches that of a nuclear emulsion, making it possible to have the advantages of the latter technique without its disadvantages. Xenon is extremely expensive, but after the first cost of filling the chamber, it can be used for an indefinite number of exposures without detriment to the liquid. It can thus do the work of thousands of stacks of emulsions, which are expensive to produce and to process after exposure. A xenon-filled chamber is being built at the University of Michigan.

The physical dimensions of a bubble chamber naturally depend on the use for which it is intended. It is hoped in the first instance to learn more about the properties of the newly discovered particles from a detailed study of reactions such as those in which protons bombarded by high-energy π-mesons produce neutral hyperons and κ-mesons, which, being uncharged, do not form tracks in the liquid. Their presence and direction are nevertheless revealed by the tracks of the pairs of charged particles into which they quickly decay. In order that these pairs of tracks shall terminate inside the liquid, the lateral dimensions of the chamber must be about 15 cm if the liquid is propane and about 50 cm if it is hydrogen; the dimension in the beam direction must be at least twice the corresponding lateral dimension. A propane chamber fulfilling these requirements costs very little more than a conventional cloud chamber of similar dimensions, and several are already in operation in the United States, Russia, and England. The development of a liquid hydrogen chamber of the dimensions quoted is far beyond the financial resources of most laboratories, but rapid progress in this direction is being made at the Radiation Laboratory, California, under the direction of Professor Luis Alvarez. A compromise, which is much less expensive, is to use a much smaller hydrogen bubble chamber to produce and identify the event, and to use other neighbouring chambers to stop the long-range products.

The analysis of the data obtained by cloud chambers and emulsions is a slow, laborious process. Much time and skilled effort are required, first to disentangle the really interesting events from the large background of unwanted tracks, and then to perform the various measurements from which velocities, charges, and momenta can be assigned to the various particles participating. Even before the advent of the bubble chamber the unsatisfactory situation had arisen in which data were being accumulated much faster than they could be analysed. With existing techniques the analysis of the photographs produced in a single day by a bubble chamber operating in the beam of a pulsed accelerator would take over a year to complete. A new analysis technique, utilizing existing electronic computers, is therefore essential.

The following technique has been evolved. Instead of re-projecting the two stereo views of the bubble tracks so as to reproduce the actual particle path in space, enlarged images of the two views are projected alongside each other on a screen. A relatively untrained person operates a mechanism controlling a set of cross-hairs so that the centre of the latter follows the direction of each track in turn. The two co-ordinates of individual bubble images on each of the two stereo pictures are punched on to a tape, which is then fed into the electronic computer. The latter gives the three co-ordinates of points along the actual particle path in the chamber, fits a curve to the points, and gives the momentum of the particle which formed the track. In a complicated scattering event it can also give the angles between the directions of the various participating fragments and solve the resulting problems in relativistic mechanics. Using this technique, the time for analysing a track can be reduced to about a minute.

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The fossil plant cuticle

T. M. HARRIS

The cuticles of fossil plants are of exceptional interest, for they have great chemical stability and in consequence they represent not fossil material in the ordinary sense, but the actual cuticle as it existed on the living plant many millions of years ago. Although this has been known for more than a century, it is only comparatively recently that plant cuticles have been used for practical purposes such as the identification of fossil plant species.

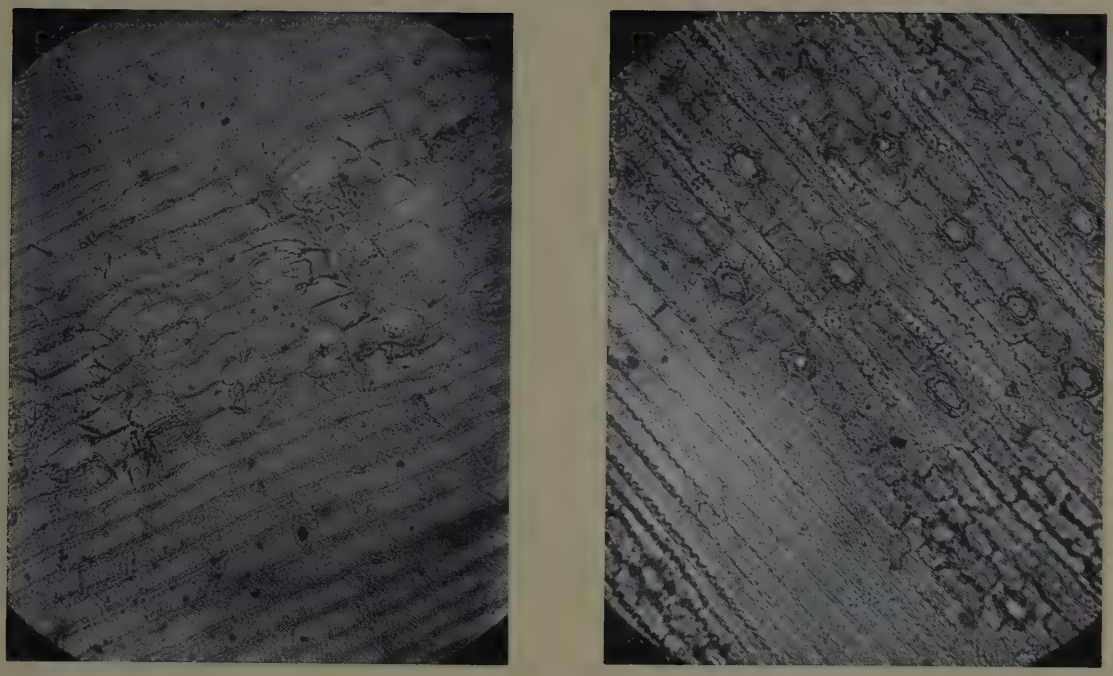
The cell walls of land plants are composed of many materials besides cellulose. Among them is cutin, which forms a tough membrane, the cuticle, outside the epidermis. Cutin is not present in the bud but appears as the leaf expands; it may thicken slowly during the life of the leaf. Cutin is of a wax-like nature and is impervious to water: the cuticle thus helps to conserve water in dry weather. Like a wax, it is readily permeated by dyes such as Sudan III, and it can therefore be readily distinguished in sections by this means. The chemical stability of cutin is remarkable and has important consequences. In the living plant this property is perhaps valuable because it forms a protective film which no organism can at all readily attack; in fossil plants it may allow the cuticle to persist unchanged through millions of years and thus to be available for examination by the fossil botanists of today. Cuticles have been recovered from some of the oldest (Devonian) plants. Finally, the great chemical stability of the cuticle makes its isolation for examination a relatively easy matter, for all that is necessary is to subject the fossil material to a chemical treatment violent enough to dissolve everything else.

Stable though it is, cutin is not entirely resistant to all natural destructive processes, and the cuticles of dead leaves may ultimately be destroyed by bacteria; but the process involved is an aerobic one. However, leaves which become fossils usually do so by falling into rivers and being buried in mud under anaerobic conditions: under such conditions the cuticle will remain intact indefinitely. But like all organic material, cutin may be destroyed by some of the more violent natural forces such as high temperatures and pressures, and thus by no means all plant fossils still possess intact cuticles.

For our present purposes we need not concern ourselves with more than the general nature of the method of isolation now commonly used in the laboratory. The fossil material, such as coal, is put into a mixture of nitric acid and potassium chlorate for a few hours, when its colour gradually changes from black to brown. The material is then rinsed and put into ammonia, when a black solution is formed and the cuticle is left intact as a transparent membrane.

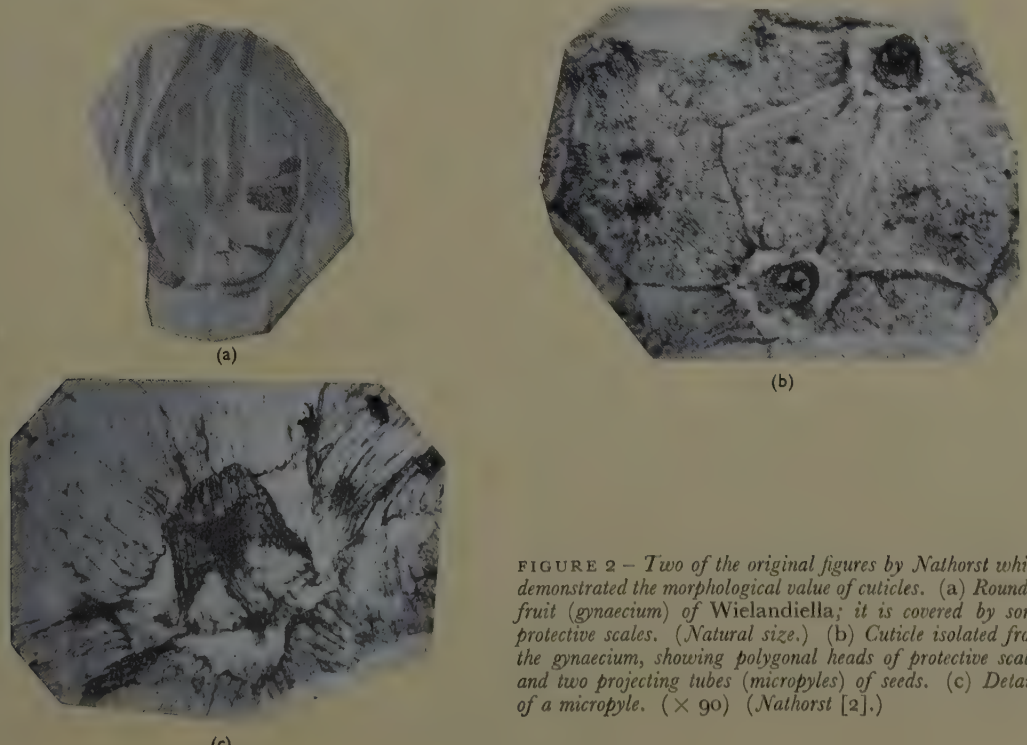
In a leaf such as a pine needle the cuticle forms a thin layer all round the epidermis, and it permeates the cellulose in the deeper layers of the epidermal cell wall. When the cuticle is isolated by a process such as that described above and is spread out on a microscope slide, the outline of every epidermal cell can be seen to be represented by a ridge. The stomata are particularly closely delineated. Thus the cuticle not only has distinguishing characteristics of its own, but to a considerable extent represents the structure of the underlying epidermis: its close study can therefore be most informative. Thus it is often possible to recognize family characters, as in the arrangement of cells round the stomata; generic characters, as in the grouping of the stomata; and specific characters, as in certain details of cell shape. Sometimes, too, the conditions under which the plant has grown can be deduced. Adverse conditions in which the leaf is growing lead to its remaining small: although it has nearly the normal number of cells, each one is comparatively small.

Again, the cuticle can help to solve one of the most vexatious problems in fossil botany—that arising from the fact that a particular fossil often represents only a small fragment of the original plant. Thus, for want of evidence to relate them, fossil remains of different organs of a single species may be assigned to several species. But sometimes the leaf cuticle may provide evidence of relationship, for a characteristic feature shown by it—such as a peculiar kind of hair—may be found on several other organs of the same plant. Again, although leaves are among the commonest of plant



(a) (b)

FIGURE 1 – *Surface views of isolated cuticles and stoma of two conifers.* (a) *Cedar of Lebanon,* C. libani. (b) *Pine,* Pinus palustris. (× 200)



(a) (b) (c)

FIGURE 2 – *Two of the original figures by Nathorst which demonstrated the morphological value of cuticles.* (a) *Rounded fruit (gynaecium) of* Wielandiella*; it is covered by some protective scales. (Natural size.)* (b) *Cuticle isolated from the gynaecium, showing polygonal heads of protective scales and two projecting tubes (micropyles) of seeds.* (c) *Details of a micropyle.* (× 90) *(Nathorst* [2].)

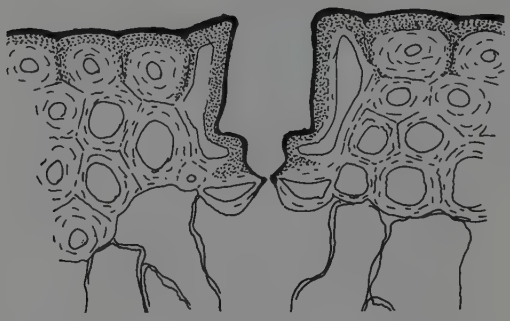


FIGURE 3 – *Section through epidermis of Scots fir,* Pinus sylvestris, *showing a stoma at the bottom of a deep pit. The strongly cutinized layers are solid black, and the weakly cutinized layers stippled.* (× 450)

fossils it is often difficult to assign them to a definite species, for although there may be much variation among the leaves on a single tree there is often no great obvious difference between the leaves of two quite distinct species. The microscopic structure of the leaf cuticle, however, may be quite specific. The precise identification of fossil leaves is important not only to the botanist but to the geologist, for the latter makes much use of them for the identification of rocks.

An interesting example of the importance of the cuticle in the identification of species is provided by certain plant fossils in the Jurassic beds of Yorkshire. Hamshaw Thomas recognized the fruits of two distinct plant species in the Gristhorpe Bed near Scarborough and pointed out that there should be two different kinds of leaf to correspond. But when the leaves, attributed to *Sagenopteris phillipsi*, were examined they seemed to vary continuously in form and thus not to fall into the two groups expected. However, when the cuticles of a large number of specimens were prepared and examined they were at once seen to fall into two well defined groups. One group had straight cell walls, the other sinuous ones. When the leaves themselves were re-examined in the light of this information it was seen that those of one group had, on the average, much broader segments than those of the other. Thus a botanical doubt was unequivocally resolved: the identification of two species of fruit was proved correct by the identification of the two corresponding kinds of leaf.

The converse also happens. A single plant may have leaves of such varied form that individual workers, to each of whom only a few specimens have been available, have attributed them to different species. In consequence the literature becomes burdened with several different names corresponding in fact to only a single species, and this confuses evidence of identification based on less variable organs such as those of reproduction. While the specific identification of fossil leaves such as these must always be to some extent a matter of opinion, the case for including them all within a single species is much strengthened if they have uniform cuticles.

The additional evidence provided by the cuticle is particularly valuable in dealing with small leaves, for their shapes are often of little value in identification. Thus the Conifers have small leaves, and the assignment of their fossil remains to definite groups was until recently in a state of hopeless confusion. Now, however, study of their excellently developed cuticles has completely changed the situation, and the fossil Conifers are, from the point of view of classification, a well defined group, and, in consequence, one very useful for the dating of other remains.

An example of this is provided by certain carboniferous quarries in South Wales, in which there are occasional fissures full of rubbly material

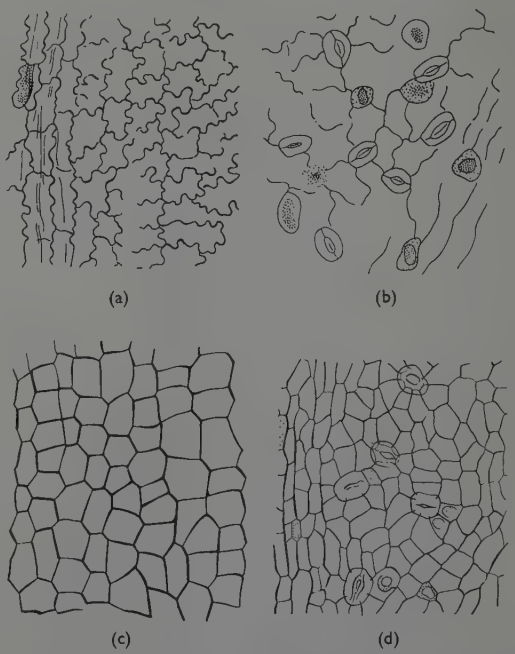


FIGURE 4 – *Cuticles of two Yorkshire species of* Sagenopteris. (a) *and* (b) *Upper and lower cuticles of* Sagenopteris colpodes; (c) *and* (d) *upper and lower cuticles of* Sagenopteris phillipsi. (× 150)

—obviously of later origin—containing bones representing an interesting fauna of small land animals. All that could be said of the age of the animal remains was that they had early Mesozoic affinities and were of an age greater than that corresponding to a stage in the Lower Lias when the sea covered the area and sealed it off. Further evidence was much needed, and a conifer proved valuable. When some of the rubble was dissolved in hydrochloric acid some tiny conifer leaves were obtained; they were only one or two millimetres in diameter and only slightly longer. After suitable preparation, however, their cuticles were found to have a clearly defined structure corresponding precisely to a species, *Cheirolepis muensteri*, which has been found abundantly in the Rhaeto-Liassic rocks of south-west Germany, but not hitherto outside this district or this fairly short geological period. This was therefore a very useful indication of the age of the associated animal remains.

If cautiously interpreted, the cuticles of fossil plants may offer useful information about the climatic conditions obtaining at the time the plant flourished. A good many fossil leaves have thick cuticles and deeply sunken stomata which often have additional protection in the form of pegs, folds of the leaf surface, and hairs. Such organization looks as though it would diminish the loss of water by evaporation, and it is certainly true that in modern plants such 'xeromorphic' features are seen more frequently in plants growing in climates where there are frequent severe droughts than in plants growing in permanently mild climates. There is therefore some evidence of a correlation between xeromorphic form and a dry climate. Notwithstanding his own earlier publications [1], however, the writer believes that although inferences based on this kind of evidence are legitimate they are nevertheless speculative.

Plant morphologists can obtain a good deal of useful information from the study of cuticles. Botanists want to understand the organization of every plant organ, and satisfactory methods, taught to students, have been worked out for modern plants. But methods such as microtomy are scarcely applicable to, say, a fossil fruit compressed to a film of coal. Here the cuticle is of extreme value in making the epidermal surfaces available for microscopic examination. The first outstanding success gained in this way was with the gynaecium (seed-producing organ) of the flower of certain Bennettitales. The latter are an extinct group, very different from any now living,

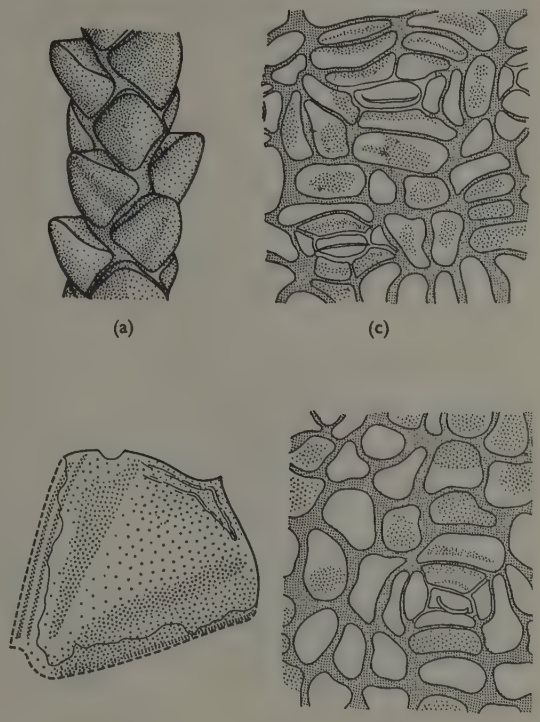


FIGURE 5 – Brachyphyllum mamillare *and* Araucarites phillipsi. (a) *Small piece of twig of* B. mamillare *in restoration* (× 3). (b) *Isolated scale of* A. phillipsi (× 2). (c) *Cuticle from pointed end of* A. phillipsi. (× 400). (d) *Cuticle of leaf of* B. mamillare. (× 300). (*Kendall* [3].)

and accordingly all our knowledge of them is necessarily derived from fossil remains. A. G. Nathorst [2] recovered some of these compressed gynaecia —discs of coal about 3 cm in diameter and 1 mm in thickness—and noted that their surfaces showed definite fine markings; their nature was, however, obscure. Spectacular results were obtained, however, when fragments of these gynaecia were macerated. It was discovered that the surface was made up of two kinds of units—hexagonal plates, which are now known to be the armoured heads of little scales; and little tubes, which are the micropyles or pollen-receiving parts of seeds. Further work has demonstrated the presence of pollen grains inside the micropyles and various cuticles around and inside the seeds.

The reproductive organs of fossil plants often exist as insignificant little specks of coal, and many of the earlier fossil botanists ignored these as uninformative. Now, however, a tiny fossil seed can

be made to yield several cuticles, each with characteristic cells, and possibly also the pollen grains concerned in its pollination.

The problem of fragmentation—the attribution of different organs of the same plant, found in isolation, to different species—has already been referred to. The task of bringing the right ones together is a difficult one, but if we decide to wait until we find a lucky specimen with all its parts joined together we must expect to wait a long time. Often the first suggestion comes from repeated association, but this merely shows that the two organs come from plants of the same kind of vegetation. Many examples could be quoted, but a recent and simple one is provided by the work of Miss M. W. Kendall [3], who has assembled the conifer shoot *Brachphyllum mamillare* with the cone-scale *Araucarites phillipsi*, which have been found together many times. The cone-scale is just like one of the seed-bearing units into which the cone of the Monkey-puzzle (*Araucaria*) falls when ripe; the shoot has tiny scale-leaves like some cypresses and very unlike that of *Araucaria*. Although an *Araucaria* cone-scale is mostly woody, it has a pointed tip which is green like a leaf when young and has an epidermis just like that on the leaf of the same plant. This proved to be so also in the fossils, the cuticle of the tip of *Araucarites phillipsi* being just like that of the leaf of *B. mamillare*, which itself is surprisingly like that of *Araucaria*. Since no other fossils in the flora have a cuticle of this kind, it was concluded that *Araucarites phillipsi* is identical with *Brachyphyllum mamillare*. Subsequently this conclusion was shown to be true by the lucky find of an intact cone on a shoot.

Fossil spores and pollen grains are preserved as cuticles, but they form too big a subject to dismiss in a few words. H. Godwin has previously discussed in this journal [4] the subject of pollen in peat, and all that can be done here is to indicate lines on which work is proceeding.

Geologically speaking, they make excellent zone fossils because they blow about widely and deposit both in marine muds near the coast and in lakes far inland. The oil geologists have found them most useful for correlating such deposits which have no other fossil in common.

On the botanical side, they prove the existence of many plants additional to those which grew beside rivers and formed ordinary fossils. Caution is, however, necessary in the interpretation of results: pollen grains are rather simple things and lose some of their character when flattened, and their identification is often difficult. Thus some workers have reported Dicotyledonous pollen grains from several Jurassic localities, but others dispute the identifications and regard these grains as Gymnosperm pollen or fern spores distorted by compression.

Although the present method of isolating the cuticle from fossil plant material is simple and convenient, it is fundamentally bad in that it completely destroys all other material. We believe that a compressed fossil must include in its coaly substance not only the cuticles but all other tissues that survived bacterial decay, and we feel, too, that we have only to examine it in the right way to be able to display all these tissues clearly.

Already methods exist. The least altered fossil plants can be softened with caustic soda, embedded, and microtomed, but the more compressed ones appear merely as a brown film with only cuticles differentiated. Thomas tried etching such sections (of *Caytonia* seeds) with fluids which would ultimately dissolve the coal. After many failures he succeeded in demonstrating certain thick-walled cells, but the method is laborious and success very rare. More hope lies in the methods of the coal petrologists, who polish and etch an apparently homogeneous piece of coal and can then demonstrate the compressed plant cells. That this has not been seriously tried with compressions is due to there being so few workers and so much work usefully to be done on present lines: there is in consequence little incentive to test new methods. However, when we do learn to display the inner tissues of an ordinary compression, fossil botany will make a further great advance.

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The generation of electricity by fishes

R. D. KEYNES

The ability of certain fishes to generate substantial electric potentials was discovered over two hundred years ago, but it has only comparatively recently become clear how the relatively small voltages produced by the individual cells in the electric organ are added together during the discharge. The discovery that some electric fishes are able to use their discharges as part of a direction-finding system has added fresh interest to the subject.

In September 1751, while travelling in West Africa, Michel Adanson [1] came across the strange fish now known as *Malapterurus electricus*, the electric cat-fish. He wrote: '*Les nègres le nomment ouaniear, et les françois trembleur, à cause de la propriété qu'il a de causer, non un engourdissement comme la torpille, mais un tremblement très-douloureux dans les membres de ceux qui le touchent. Son effet ne m'a pas paru différer sensiblement de la commotion électrique de l'expérience de Leyde, que j'avois déjà éprouvée plusieurs fois. . . .*' This occasion, preceding by some 35 years Galvani's famous observations, seems to have been the first on which the electrical properties of the fish were recognized as such, although the disconcerting consequences of handling it incautiously had long been known. The other fish mentioned by Adanson, *Torpedo*, was familiar to the Romans and Greeks—Scribonius recommended its use to cure chronic headaches and gout—and its discharge was first described as electric by John Walsh [2] in 1773. Two years later, there appeared in the Transactions of the Royal Society a letter to Walsh from an American physician, Hugh Williamson [3], concerning some experiments carried out in Philadelphia on the discharge of the 'electrical' eel, *Electrophorus* (formerly *Gymnotus*) *electricus*. At Walsh's instigation, John Hunter dissected *Torpedo* and *Electrophorus* [4], and his specimens of *Torpedo* are still preserved in the museum of the Royal College of Surgeons. Photographs of two of them are shown in figure 1; they reveal admirably the kidney-shaped electric organs, built up of numerous columns of thin hexagonal 'electroplates', stacked one on another like a pile of pennies, and innervated by four large nerve trunks arising from the electric lobe of the brain.

During the 180 years since Hunter made his dissections, the electric organ has excited the interest of many physicists and physiologists; Franklin, Cavendish, Volta, Davy, du Bois-Reymond, Faraday, and Bernstein are only a few of the eminent scientists who have worked with electric fishes. Most of the early work was concerned in establishing that electricity from 'animate' sources was the same as that from 'inanimate' ones, and in making detailed studies of the anatomy of the electric organ. Several further kinds of electric fish were discovered, including one more with a fairly powerful discharge (*Astroscopus*, the star-gazer of North America, first described by U. Dahlgren in 1906) and, from anatomical evidence, others whose discharge is relatively weak (the rays and skates, a family of African fishes called mormyrids, and the South American gymnotids, closely related to *Electrophorus*). Probably because the discharge of the electric organ was easier to detect, with the relatively insensitive electrical measuring devices available during the nineteenth century, than the smaller voltages produced by muscle and nerve, an almost disproportionate amount of attention was paid to it, judging from the length of the chapters on its properties in the textbooks of about 1900. Yet when it is realized that even with a whole *Malapterurus* at his disposal, du Bois-Reymond [5] had to make his measurements with the device illustrated in figure 4, whose reliability cannot have been of the highest order, it may partly be understood why these same books had little to offer in the way of good explanations of the origin of animal electricity.

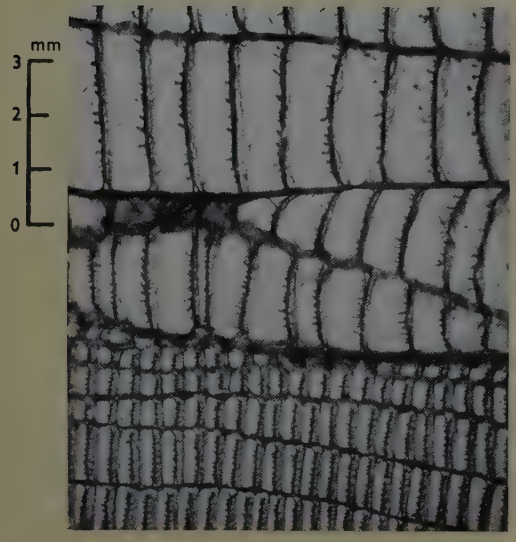
In all electric fishes the electric organ consists of large numbers of disk-like cells called electroplaxes or electroplates, each having a nerve connected to one surface but not to the other. The electroplates are arranged in orderly columns, with their innervated sides all facing in the same direction. In *Torpedo* the electroplates lie in the horizontal plane, and are packed very tightly together, forming a wide and thin electric organ whose unit cells discharge in parallel rather than in series, as befits a marine fish living in a medium whose electrical resistance is relatively low. With the exception of *Astroscopus*, the other electric fishes have vertical

electroplates, usually separated by quite large spaces and arranged more in series than in parallel. As may be seen from figure 2, the surfaces of the electroplates are often studded with prominent papillae, whose function is presumably to increase the total surface area and hence to lower the effective internal resistance of the organ. The extreme example of specialized development is provided by *Electrophorus*, where the greater part of the lateral four-fifths of the fish is occupied by the electric organ (figure 3). This huge mass of electric tissue is made up of about 70 columns of electroplates, each containing no fewer than 6000 cells in series. On open circuit (i.e. in air) a large electric eel can produce brief (3 msec) pulses of up to 600 volts in potential; short-circuited, the peak current is of the order of 1 amp. The maximum power output is rather more than 100 watts—about half an ampere at 200–300 volts. A large *Torpedo* may generate a current of several amperes at around 50 volts, so that in terms of power output this species is the most potent of the electric fishes. At the other end of the scale, the mormyrids, the gymnotids other than *Electrophorus*, and the rays, have much smaller electric organs, in the form of spindle-shaped structures replacing certain of the caudal muscles, and are capable only of discharges of the order of one or two volts. The discharges of *Astroscopus* and *Malapterurus* are intermediate in size.

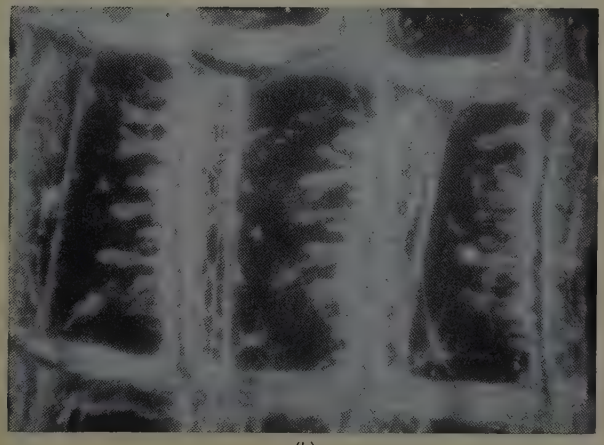
The problems which have, perhaps, intrigued physiologists the most, have been to explain how the additive discharge of the electroplates is achieved, and what is the source of the energy dissipated while electric current flows. Until 1900, there was no convincing answer to either question, but at about this time Bernstein [6] made the inspired suggestion that the surface membranes of the electroplates were polarized so that the interior of each cell was negative to the exterior, and that during the discharge the potential across the innervated face collapsed, leaving that across the non-nervous face unaltered. However, although he did some very interesting physical experiments on *Torpedo* [7], which provided strong evidence that the immediate source of energy for the discharge was a pre-existing ionic concentration gradient rather than a chemical reaction, he had no means of testing his main hypothesis. As often happens in physiological research, the problem could not be solved until techniques were available for studying the behaviour of single cells. The appropriate method in this case was the employment of glass micropipettes, 0·5 μ in diameter at the tip, filled with potassium chloride, of the type originally developed by G. Ling and R. W. Gerard [8] in Chicago, which are now being applied extensively for the determination of intracellular potentials. By using pairs of such microelectrodes, connected via a differential direct-coupled amplifier to a cathode-ray oscillograph, and inserting one of them into the individual electroplates in a slice of electric organ, it has recently been shown by H. Martins-Ferreira and the author [9] (working in Professor Chagas's laboratory in Rio de Janeiro), and by H. Grundfest and his colleagues [10] in New York, that, at least for *Electrophorus*, Bernstein was not far from the mark. As may be seen in figure 5, the inside of the resting electroplate is indeed negative to the outside, by some 90 mV, and Bernstein was wrong only in that the potential across the nervous face does not merely collapse during activity, but is actually reversed by about 60 mV. The potential across the non-nervous face barely alters, so that each electroplate contributes 150 mV to the total discharge, in the manner indicated in figure 6.

Investigations on the embryology and comparative anatomy of the electric organ long ago showed that, except in the case of *Malapterurus*, the electroplates are derived from muscle fibres, or perhaps from the special junctional regions called 'motor end-plates', where the motor nerves make contact with the muscles, and where the incoming nerve impulse sets up a corresponding propagated action potential in the membrane of the muscle fibre. It has sometimes been assumed that a study of the electric organ would lead the way to an understanding of the mechanism of neuromuscular transmission, but in fact the reverse has happened, since the elegant work of B. Katz, P. Fatt, J. del Castillo, and others [11] in University College, London, has revealed appreciably more about the properties of the motor end-plate than is known about the electroplate. The main difference between electrical activity at a motor end-plate and that occurring during conduction of an impulse along a nerve or muscle fibre, is that the former depends on the release of a chemical transmitter, acetylcholine, from the neighbouring nerve endings, and cannot be elicited by applied electric currents. On the other hand, nerve and muscle membranes are unaffected by acetylcholine but are electrically excitable. The propagation mechanism depends intrinsically on the spread of electric currents ahead of the advancing impulse. Another difference which is important in the present context is that the depolarization caused by acetylcholine

FIGURE 1 – *Two specimens of* Torpedo *dissected by John Hunter to reveal the electric organs and their nerve supply.*



(a)



(b)

FIGURE 2 – *Photomicrographs of sections through the electric organ of* Electrophorus electricus. (a) *is taken at a place where the organ of Sachs (electroplates widely spaced) overlaps the main electric organ (closer spacing). For* (b) *the magnification is about five times greater than for* (a), *to which the scale refers. In this species the electroplates are innervated on the side facing the tail of the fish* [9].

(a)

(b)

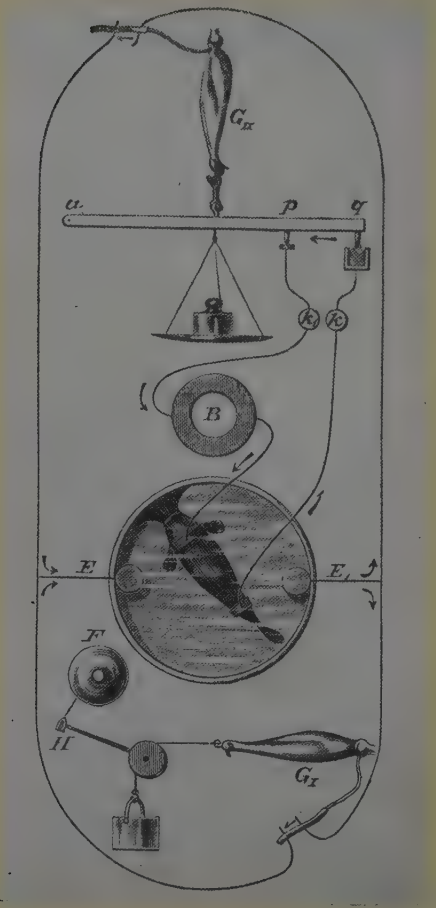


FIGURE 3 – (a) *A living electric eel and* (b) *a section through the main electric organ. In the uppermost third of the body are the swimming muscles, spinal cord and swim-bladder, while translucent columns of electroplates fill the remainder. Beneath the main organ is a subdivision of the electric organ named after John Hunter.*

FIGURE 4 (*left*) – *du Bois-Reymond's frog-alarum and frog-interrupter. One frog nerve-muscle preparation* (G_I) *was used to ring a bell when the fish discharged, while another* (G_{II}) *served to disconnect the galvanometer* (*B*) *after the first pulse of the group had been measured.*

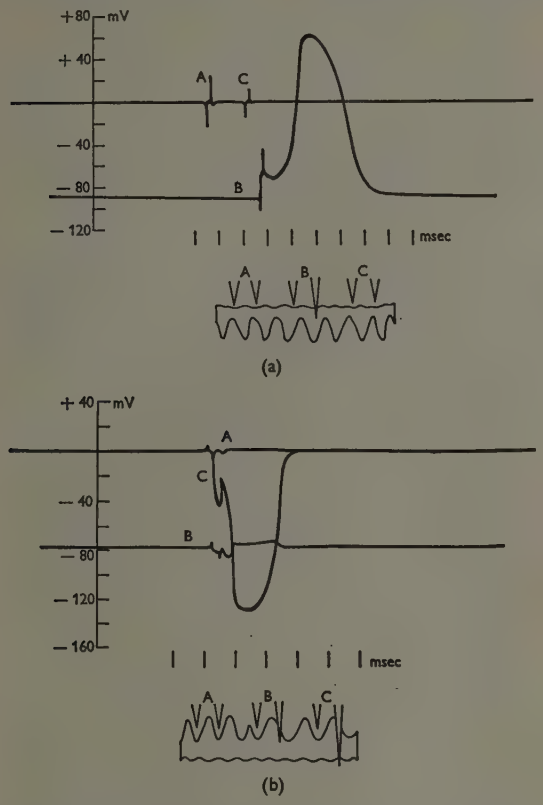


FIGURE 5 – *Microelectrode recordings of the membrane potentials in the electroplates of* Electrophorus electricus, *approaching (a) through the innervated face, (b) through the non-nervous face (indicated diagrammatically by the presence of papillae). The action potential is preceded by a stimulus artifact, which was not perfectly synchronized on successive sweeps* [9].

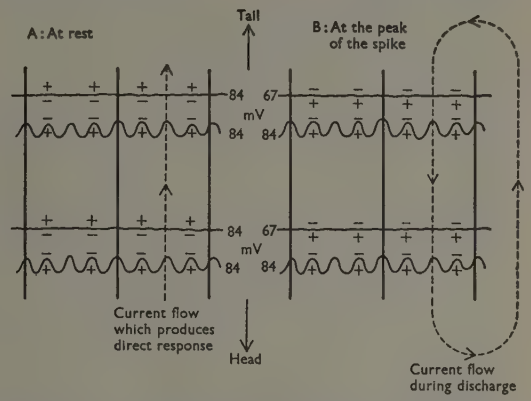


FIGURE 6 – *A diagram illustrating the way in which the electroplates of* Electrophorus *discharge additively. The figures are average results for a number of specimens* [9].

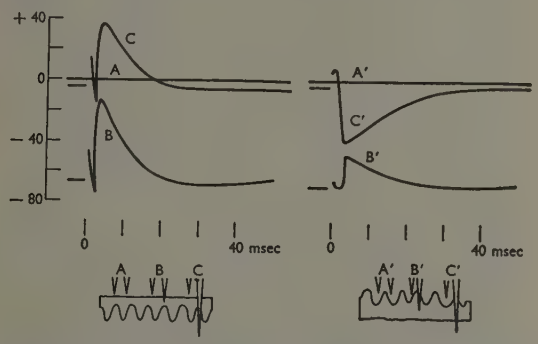


FIGURE 7 – *Microelectrode recordings of the membrane potentials in electroplates of* Raia clavata. *In this species there seems to be, in contrast to the state of affairs in* Electrophorus (*figure* 5), *an appreciable voltage drop across the non-nervous face; note also the difference in time scale and shape of the response* [24].

at the end-plate consists in a reduction of the membrane potential towards zero in the fashion predicted by Bernstein, and does not involve the substantial reversal in polarity which is observed elsewhere in nerve and muscle. Since in *Electrophorus* there is certainly a large reversal in potential (figure 5), and since, as was first shown by D. Albe-Fessard and her collaborators [12], the nervous face of the electroplate can be directly triggered by applied electric shocks, it has been concluded that the electroplate should be regarded as a modified muscle fibre, not as a modified motor end-plate. The distinction has been amplified by Grundfest's recent work [10], which suggests that the mainly muscle-type membrane of the nervous face is interspersed with junctional regions which have much in common, both in electrical behaviour and in function, with motor end-plates.

In other species the situation may be different, and in *Torpedo* and *Raia* it is probable that the electroplates can legitimately be thought of as greatly overgrown motor end-plates, containing little or no muscle-type membrane. Microelectrode recordings in *Raia* (figure 7) have shown that here the potential across the nervous face is not reversed to any great extent during activity, and its time course is strikingly like that of an end-plate potential. In these two elasmobranch fishes, moreover, the electric organ is not directly excitable, and can be made to discharge only by stimulating the attached nerves; also, in contrast to *Electrophorus*, treatment with the drug curare can put the electric organ completely out of action. However, it is not surprising that there should be some variation in the mode of discharge of individual electric organs, since they have evidently

been evolved quite independently in the various families of electric fishes, and there is no reason why their evolution should have followed an identical course in every case.

The question as to what gives rise to the initial polarization of the cell membrane, and to the change in potential across the nervous face during activity, can be answered only by analogy with nerve and muscle, whose electrical properties have been studied much more intensively with modern techniques than have those of the electric organ. The basis for A. L. Hodgkin's ionic hypothesis of nervous conduction [13] is that all excitable tissues are found to contain a high internal potassium concentration and low internal sodium concentration, as compared with the high sodium and low potassium of the body fluids in which they are bathed. There is evidence that the electric organ of *Electrophorus* is no exception in this respect [14]. The resting membrane potential may be said to arise from the potassium concentration gradient, since the quiescent membrane behaves as if it were almost exclusively permeable to potassium ions. The action potential has been shown to result from a large but strictly transient increase in the permeability of the membrane towards sodium ions. The immediate source of energy to provide the currents which flow during propagation of an impulse—and hence, in all probability, during the discharge of the electric organ—is the entry of a small quantity of sodium into the cell, followed by the leakage of an equal amount of potassium from it. The consequent mixing of the ionic contents of the cell with those of its surroundings must later be reversed, and this appears to be achieved by an active transport mechanism which draws its energy supply from cellular metabolism and is capable of simultaneously extruding sodium and absorbing potassium against the concentration gradients [15]. However, although the working both of the conduction mechanism and of the so-called 'sodium pump' have been examined in some detail in a variety of excitable tissues, establishing beyond doubt that the postulated sequence of permeability changes and the ensuing uphill transfer of ions do occur, it must be added that there is as yet no indication concerning the precise nature, on a molecular scale, of the processes involved in the passage of sodium and potassium ions across the cell membrane. It should be noted that the permeability changes caused by the release of acetylcholine at the motor end-plate are somewhat different from those outlined above [11], but that the mixing of ions is again probably the immediate source of energy for the potential changes.

There is one electric organ—that of *Malapterurus*—to which much of what has just been said apparently does not apply, because in this species the electroplates are thought to be derived from glandular tissue, not muscle. *Malapterurus* is also aberrant in that the innervated faces of the electroplates become electrically positive during the discharge, not negative as in all other electric fishes (see figures 5 and 7). This suggests either that the initial resting potential across the nervous face has a normal polarity (inside of cell negative) but increases during activity instead of decreasing or being reversed, or that the membrane potential decreases during activity but is initially in the opposite direction (inside of cell positive) to that in nerve and muscle fibres. Both explanations would involve ionic movements unlike those that have been studied elsewhere, and it will not be possible to decide between them until the electric organ of this interesting fish has been investigated with microelectrodes.

It is clear that in no case does the electric organ discharge spontaneously; it is always under the control of the central nervous system. Even in the few electric fishes which produce a continuous series of pulses at a fixed repetition rate which is independent of what they are doing at any moment, local cooling of the brain has been shown to reduce the frequency [16]. The anatomy of the motor pathways from the brain to the electric organ has received some attention, and most electric fishes have been found to have particularly large nerve cells in their spinal cords (or, in *Torpedo*, in the brain itself), which give rise to the nerves connected to the electroplate. In *Torpedo* all parts of the electric organ are roughly equidistant from the brain, but the question arises why, in a fish as long—perhaps six feet—as *Electrophorus* may be, there are not serious differences in overall conduction time between nerve impulses triggering the opposite ends of the organ. As was shown by C. W. Coates, R. T. Cox, W. A. Rosenblith, and M. V. Brown [17], the whole organ in fact discharges almost synchronously, as it has to do if the maximum voltage is to be achieved. This problem has recently been examined by D. Albe-Fessard and H. Martins-Ferreira [18], who have found that the discrepancies in conduction time along the spinal cord are compensated in several ways, so that instead of the initiation of the discharge being spread over a calculated 12 msec, it is compressed within a period of about 1·5 msec.

It is interesting to speculate how the discharge of *Malapterurus* is synchronized, since this species is, as in other respects, unique in having all the electroplates in each half of its electric organ innervated by the branches of a single nerve fibre, which would seem to rule out some of the compensation mechanisms described for *Electrophorus*.

Not the least interesting aspect of the physiology of electric fishes is the use they make of their electric organs. One has only to throw a frog into a tank full of electric eels, and to watch it being stunned and swallowed, to convince oneself that *Electrophorus* employs its electricity offensively, but this kind of observation is less easy to make with *Torpedo*. However, D. P. Wilson [19] at Plymouth has persuaded specimens of *Torpedo nobiliana* in an aquarium to attack dead fish towed through the water on a wire, and has described the way in which the prey is enveloped by the pectoral fins of the *Torpedo* before it discharges. There is surprisingly little direct evidence that the other fishes with relatively large electric organs do habitually use their powers for offensive purposes, though it has been suggested that *Malapterurus* employs its discharge to make other fishes disgorge their food. Since all electric fishes seem to discharge most readily when touched or alarmed in any way, it is possible that in many species the main role of the discharge is defensive, and Wilson [19] has seen *Torpedo* apparently discharging in order to drive away intruders. More investigations of the mode of life of electric fishes are needed to settle this point.

As far as the small electric fishes are concerned, an important new field of research has recently been opened up with the discovery by H. W. Lissmann [20] in Cambridge, and by C. W. Coates and his colleagues [16, 21] in New York, that *Gymnarchus niloticus* and various mormyrids and gymnotids produce a continuous series of pulses which seem to serve the purpose of a direction-finding transmitter. In *Gymnarchus* the repetition rate is remarkably constant at about 300 pulses/sec, but in most other species the pulse frequency varies from time to time, perhaps with the degree of interest taken by the fish in its surroundings. This is particularly obvious in the case of *Electrophorus*, which produces (probably from that part of the tail end of its electric organ where the electroplates are most widely spaced, called the organ of Sachs) small direction-finding pulses as well as the lethal groups of large pulses already described [9]. A stationary electric eel is electrically silent, but as soon as it begins to move, it transmits pulses at rates up to about 50/sec [22]. Lissmann [20] has shown that *Gymnarchus* can differentiate between conductors and non-conductors placed in the water beside it, in all probability because it is extremely sensitive to changes in the pattern of electric current flow in the water around it during the discharge. It is not yet known how the sensory side of the direction-finding system works, nor even where the detectors are located, apart from the observation of Coates [22] that lacquering the head of *Electrophorus* interferes with its direction-finding abilities.

Charles Darwin [23] found difficulty in explaining the evolution of the electric organ, because of the apparent absence of any transitional stage between no organ and the extreme development of one in fishes like *Electrophorus*. The existence of small direction-finding transmitters in the gymnotids and mormyrids helps to bridge the gap, but by no means solves the whole problem, since there is no evidence that in the other four kinds of electric fish (*Torpedo*, the rays and skates, *Astroscopus*, and *Malapterurus*) the electric organ is ever used for direction-finding. In any case, the first three of these families live in salt water, where one would expect the range of an electric direction-finding system to be very limited. The evolutionary history of the electric organ remains an unsolved, but most interesting, question.

ACKNOWLEDGMENT

I am indebted to Miss J. Dobson, Mr Edwards, and the Royal College of Surgeons for the photographs in figure 1; to Dr A. Couceiro for those in figure 2; and to the *Journal of Physiology* for permission to reproduce figures 2, 5, 6, and 7.

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Book reviews

ASTRONOMY FOR AMATEURS

Atlas du Ciel, *by Vincent de Callataÿ. Pp.* 157. *Les Éditions de Visscher, Brussels.* 1955. *Belg. fcs* 450 *net.*

This atlas has been designed for amateurs who wish to observe the sky and to identify particular objects without optical aid. It contains 45 plates, in which the stars are shown as white spots on a black ground, to simulate as nearly as possible the actual appearance of the sky. The old mythological constellation figures are not shown, nor are any identifications given on these charts, but the brightest stars are connected by fine lines to assist recognition. Nine of the plates are in the form of planispheres, depicting the sky as seen from different latitudes; the remainder, which are on a larger scale, cover the entire sky in detail. No stars fainter than the 5th magnitude are included.

Accompanying the plates are small-scale charts, on which the names of the constellations and their boundaries, as fixed by the International Astronomical Union, are given, as also the names or designations of the brighter stars. The principal objects of interest in each constellation are listed and described. Appended to each plate is some textual matter relating to some object or objects in the area of the sky concerned. These textual comments have been planned to give collectively a brief elementary descriptive account of modern astronomy. They are not given in a logical sequence, but a key has been provided for the benefit of beginners, indicating the order in which they should be read.

The atlas can be strongly recommended to those who wish to star-gaze without optical aid. The first nine plates form its least satisfactory feature, the magnitudes of the stars on them not being at all adequately distinguished by the sizes of the star disks; they serve, however, to show the relative positions in the sky of the various constellations.

H. SPENCER JONES

COMBUSTION

Fifth Symposium (International) on Combustion, *The Combustion Institute. Pp. xxvi* + 802. *Reinhold Publishing Co., New York; Chapman and Hall Limited, London.* 1955. 120*s. net.*

Since the war, three major combustion symposia have been held in America, at the University of Wisconsin in 1948, at Pittsburgh in 1952, and this last at the Massachusetts Institute of Technology in 1954. At the Pittsburgh meeting the emphasis was deliberately placed on the more physical aspects of combustion, and at Massachusetts on combustion in engines and on combustion kinetics.

There are eleven review articles, six of them on problems connected with various types of engine and five on kinetics, together with ninety original papers. Of the 101 contributions 59 are from the U.S.A. and 24 from Great Britain. Many of the original papers describe work which has been or will be published elsewhere, but as the reputation of the symposia grows there is an increasing tendency for authors to publish only in the symposium proceedings, now controlled by the new Combustion Institute, so that the volumes become essential as the only source of some original work as well as a most valuable and fairly complete guide to current research trends. A minor weakness in presentation is the absence of abstracts with the papers.

A. G. GAYDON

NUCLEAR PHYSICS

Introductory Nuclear Physics (*second edition*), *by David Halliday. Pp. ix* + 493. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 60*s. net.*

There are now several elementary books on nuclear physics, but for sheer scope this book is almost certainly unbeaten. No part of the subject that this reviewer can think of is not given at least a mention, and the formidable list of references seems complete to the end of 1954. Here truly is physics. To say that the book is well written, with clear diagrams and an excellent index, would appear to place it beyond criticism.

This is not so, however. A consequence of the attempt to cover so much is that on almost every page one finds the frustrating phrase 'it can be shown'. Furthermore, references as to where

it is shown are frequently to original publications, which are several removes in difficulty from this book, even when the matter has in fact long since been treated in review articles or books. A sensible selection of books and articles for further reading would certainly be more useful to the student than the list of references given. And it would almost, though not quite, nullify the above criticism.

A strange inclusion in this second edition is a short chapter on elementary quantum mechanics. A student who does not know a good deal more quantum mechanics than is given there should not even start on this book.

L. R. B. ELTON

FUNDAMENTAL PHYSICS

Niels Bohr, and the Development of Physics, *edited by W. Pauli, with the assistance of L. Rosenfeld and V. Weisskopf. Pp. vii* + 195. *Pergamon Press Limited, London.* 1955. 30*s. net.*

Two of these essays (Darwin, Heisenberg) are historical, while the remainder, by leading figures from seven countries, look to the future and treat problems on the open frontiers of quantum theory. True to its purpose, the *Festschrift* provides a feast of information on the current position at many growing points of fundamental physics, such as the relation of quantum theory and relativity, quantum electrodynamics, superconductivity, and the nucleus.

But there is a sting, for the spirit of Bohr haunts the feast, ironically reminding us of what is lacking today. Many of the essayists say, in effect, that the Age of Bohr is nearly over, that the power of the Correspondence Principle is waning, and that theoretical research is being forced to rely more and more on mathematical virtuosity. The report on the latest work in the quantum theory of fields (Landau, from Moscow) warns us that far-reaching changes may be necessary in the theory of mesons. Yet it is becoming increasingly doubtful whether the help needed for this and other pressing tasks can be obtained from mathematical considerations alone. An improved version of atomism, purged of some unnecessary feature still lurking in present methods, and a more profound epistemology of measurement may be required for the step which will reduce current complexities and open up the next Age.

L. L. WHYTE

CHEMICAL EQUILIBRIUM

The Principles of Chemical Equilibrium, *by K. G. Denbigh. Pp. xxi* + 491. *Cambridge University Press, London.* 1955. 42*s. net.*

Professor Denbigh has communicated much of his enthusiasm for thermodynamics in a thoughtful and stimulating text-book intended for students of chemistry or chemical engineering in the last year of their degree courses. Theoretical principles are discussed fairly fully, and their applications are illustrated by over a hundred problems, many of them chosen from the examinations for the Cambridge University chemical engineering degree, together with answers and comments.

Part I (The Principles of Thermodynamics) establishes from the First and Second Laws the significance of the various thermodynamic functions and their derivatives, which are used in Part II (Reaction and Phase Equilibria) to discuss reactions involving gases, the phase rule, ideal and non-ideal solutions, and ionic equilibria. In Part III (Thermodynamics in relation to the Existence of Molecules) statistical mechanics is developed in terms of the Gibbs ensemble to include monatomic gases, perfect crystals, and the Third Law, and brief introductions to chemical kinetics, transition-state theory, regular solutions, and adsorption. Particularly useful treatments are those of the conditions of equilibrium for several independent reactions, the derivation of the phase rule, and the relation between the kinetic expressions for the forward and reverse components of a reaction. Some readers, however, may be disappointed not to find more information about the statistical calculation of equilibrium constants and more guidance on where to seek reliable numerical data.

K. W. SYKES

THEORY OF RESONANCE

Resonance in Organic Chemistry, *by G. W. Wheland. Pp. xiii* + 846. *Chapman and Hall Limited, London.* 1955. £6 *net.*

Professor Wheland's earlier book, *The Theory of Resonance*, was published in 1944 and gave the first comprehensive account of these new ideas in their application to organic chemistry. The present book, which entirely supersedes the older one, is a notable addition to the literature, since, with relatively minor omissions, it covers the whole field of resonance in organic chemistry, including structure and reactivity; furthermore the usage of the word resonance is enlarged to cover the alternative theory of molecular orbitals. This is an entirely desirable addition, since we now know enough of both the limitations and successes of the valence-bond and molecular-orbital types of approximation to distrust either unless both agree. Wheland himself has been in this field since its beginning and writes with authority. He is particularly clear in his evaluation of resonance as a phenomenon or as a way of thinking and talking about molecules. There is none of the slipshod argument which has so often dogged discussion of the applications of resonance in the past. There is a full collection (90 pages) of experimental bond lengths and bond angles, which will enhance the value of the book to some of its readers. This volume deserves the same success as its predecessor.

C. A. COULSON

ROGER ADAMS

The Roger Adams Symposium, *prepared by C. S. Marvel. Pp. ix* + 140. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 30*s. net.*

The influence of Roger Adams on the development of chemical teaching and of research and its application has been unsurpassed in the United States and has extended directly and indirectly in every direction. He has manufactured chemical doctors on the grand scale, and helped them to publish their work and fit themselves for industrial activities. Furthermore, he has penetrated every nook and cranny of the public service, wherever chemistry is relevant. The six papers presented at a symposium in his honour are contributed by former Ph.D. students (1918–29) and are all of individual interest, while together presenting a cross-section of Adams' interests. Needless to say there are many gaps, but that was inevitable in the circumstances.

The president of the Abbott Laboratories, Ernest H. Volwiler, depicts clearly the endearing qualities and outstanding achievements of one whom he justly describes as the acknowledged leader of American chemistry. The other five papers are concerned with advances in knowledge made by the respective authors. The longest section, by Wallace R. Brode of the National

Bureau of Standards, is a most useful monograph on the steric effects in dyes, a subject that might easily be overlooked in a discussion of the relation of molecular structure and light absorption. The idea of group interference in space is very significant here, and Adams' studies in this region were fundamental. Professor Johnson of Cornell University gives a clear account of his remarkable work on the unusual gliotoxin molecule, and Professor McElvain, University of Wisconsin, discusses the chemistry of nepetalic acid, a curious derivative of *cyclo*pentane. Professor Shriner of the State University of Iowa deals with some new reactions of pyrylium salts. The final paper, by Wendell M. Stanley of the Virus Laboratory, University of California, is a stimulating exposition of chemical studies on viruses. Professor C. S. Marvel, for many years a colleague of Adams, has suggested, in the wide range of topics, a corresponding breadth of outlook of the man honoured.

The present volume can be warmly recommended to the many friends of Roger Adams throughout the world. But the appeal is wider because of the absolute value of all the contributions to this outstanding two-day symposium.

R. ROBINSON

BIOCHEMICAL SYNTHESIS

Biochemical Preparations, Volume 4, *edited by W. W. Westerfield. Pp. vii* + 108. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 30*s. net.*

With the appearance of this volume, 'Biochemical Preparations' is on the way to becoming as well recognised as 'Organic Syntheses'. The series offers to the biochemist carefully checked methods of preparing substances not always easily accessible to him. For some to whom small supplies of even the commonest biochemical substances are unavailable they provide means of preparation relatively cheap in starting materials. The present volume describes the preparation by synthesis, by use of enzymes, or by isolation, of 21 substances, among which are included α-*d*-galactose-1-phosphate, α-*d*-glucose-1-phosphate, homogentisic acid, lecithin, α-lactalbumin, alcohol dehydrogenase, urocanic acid, and glutamic acid. The commendable features of each method are the footnotes, which should help in the avoidance of difficulties, and the description of the properties and evidence of purity of substances. Alternative procedures are given for the preparation of *d*-glutamic acid; in one, Crookes strain of *Escherichia coli* serves as a source of decarboxylase for the destruction of the *l*-antipode, and in the other *Clostridium perfringens*. There is something to be said for the duplication of biochemical preparations in that it allows a worker to choose one that he can carry out with the facilities he has at hand and to try out another if he fails with one. Although the series will largely be used by research workers, it should provide many useful examples of preparations for the practical instruction of students.

J. R. P. O'BRIEN

PHYSIOLOGICAL CHEMISTRY

Cole's Practical Physiological Chemistry (*tenth edition*), *revised and rewritten by E. Baldwin and D. J. Bell. Pp. x* + 263. *W. Heffer and Sons Limited, Cambridge.* 1955. 21*s. net.*

Not a few biochemists and physiologists in the early years of this century have had their first introduction in physiological chemistry through the medium of Cole's book. The present edition, following the ninth after some twenty years, is appropriately dedicated to his memory. It retains the essence of earlier editions: principles are well explained, well illustrated, and further exemplified by experiments of a simple direct nature. There has been some rearrangement of chapters and extensive rewriting. Still, many of the original experiments are retained and some remodelled; all are concerned with readily accessible materials. The authors frankly state that the analytical methods discussed are not the most up to date nor the most accurate, but are those which have been well tried and which can prove successful in the hands of students using simple apparatus. It is a book that will give a student, particularly one who has medicine in mind as a career, a sound practical introduction to elementary physiological chemistry in its qualitative and quantitative aspects. It may be that this is the right objective for students for whom a familiarity with the fundamental characteristics of biological substances is all that is required in their careers. The essence of Cole is still there; the clear and direct introductory explanations to the practical experiments and the valuable instructive footnotes, now not so profuse, to experiments.

J. R. P. O'BRIEN

GEOLOGY

L'Évolution de la Lithosphère. I. Pétrogenèse, *by H. Termier and G. Termier. Pp.* 653. *Masson et Cie., Paris.* 1956. *Paper covers, fcs* 8000 *net; cloth, fcs* 8800 *net.*

One cannot but admire the industry of the two authors when one reflects that this monumental work forms only one part of a projected series of four volumes which together will make their *Traité de Géologie*. The present volume is the second of the series and deals with the origin of igneous and metamorphic rocks. It is distinguished by the insistence of the authors that petrological problems are most fruitfully approached with their geological setting in mind. To this end a valuable synthesis of recent studies of the field-relations of rocks has been compiled to illustrate the authors' arguments. While the Termiers have not neglected their own and their colleagues' work in North Africa, they have brought together illustrations from literally every quarter of the globe. It is to be regretted that we are not given a more critical review of some of this work. For example, the transformist interpretation of the Bushveldt complex is cited at length, and the unwary reader might suppose that no other view was tenable.

The earlier chapters deal in a clear and original manner with such topics as crystal structure and crystal growth, geochemistry, the sources of energy within the earth, and the age of the earth. In the main part of the work an acquaintance with the basic facts of petrology is assumed, but to a reader with that acquaintance this book can be recommended as a fascinating study of the geology of the hard rocks. The text is clear and the maps and diagrams are excellent—perhaps more could have been included with advantage.

H. H. READ

STRATIGRAPHIC GEOLOGY

Stratigraphic Geology (*fourth edition*), *by M. Gignoux, translated by G. G. Woodford. Pp. xvi* + 698. *Bailey Brothers and Swinfen Limited, London; W. H. Freeman and Company, California.* 1955. $9.50 *net.*

In reviewing a work as gigantic as this it would be easy to write only criticisms. One knows that the late Professor Gignoux made mistakes in his first edition and did not correct all of them in the three subsequent printings. Sometimes he failed to include the results of new work which drastically

modified earlier conclusions, and occasionally he incorporated such changes in a part of his book without allowing for their effect elsewhere. Whatever criticisms a reviewer might make of the original book would apply equally to this translation. Moreover, any translator of a geological work published even five years previously is faced with the problem of whether to rewrite certain parts or to perpetuate ideas which have in the meantime become obsolete. Thus, by retaining unchanged Gignoux's classification of the Pliocene and Pleistocene, the book becomes at variance with the unanimous recommendations of a committee of the International Geological Congress.

The translation follows too closely the French idiom and consequently rarely lets one forget the original source, while the illustrations have not been redrawn but have been photographed from the French editions, with the result that the diagrams lose in clarity.

Nevertheless, Gignoux's *Géologie Stratigraphique* is not merely the only book of its type, it approaches to being a masterpiece. It is invaluable to the student, professional or amateur, and this translation has made it available to a host of readers who otherwise might have been unable to appreciate it adequately. For doing this the publishers and the translator deserve our gratitude.

F. W. SHOTTON

GENETICS AND METABOLISM

Genetics and Metabolism, *by R. P. Wagner and H. K. Mitchell. Pp. xi + 444. John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 60*s. net.*

The rapid approach of genetics and biochemistry to one another has led recently to the appearance of a number of books dealing with the combination of the two. The present book may most simply be described as complementary to Haldane's 'Biochemistry of Genetics', each filling the gaps in the other. The introductory chapters are the least satisfactory. They begin with the gene, but the gene is not the beginning of genetics: it comes at the half-way point. It demands, for example, a better understanding of meiosis than the authors offer. The telegraphic American abstracting style which they use is sometimes ill-constructed and obscure. Ideas of theory and scientific method have also troubled the authors too little: if they would drop their 'proofs' and consider the evidence they would both learn and teach their subject better. As it proceeds, however, the book improves in scope and understanding. It brings together for the first time a large and connected body of knowledge, both solid and speculative. Its influence among research workers should be far-reaching and good.

G. D. DARLINGTON

EMBRYOLOGY

Principles of Embryology, *by C. H. Waddington. Pp. x + 510. George Allen and Unwin Limited, London.* 1956. 45*s. net.*

It is a curious fact that a hundred years ago the distinction between the science of embryology and of genetics was blurred, for Darwin, following the Hippocratic writer, conceived of the resemblance between parent and offspring in terms of little particles contributed from all parts of the body of the parent which were supposed to control the production of the corresponding parts of the offspring. By this means it was hoped to explain not only hereditary resemblance but embryonic development.

Then came the great analyses of genetics by Mendel and of embryology by Roux, as a result of which genetics specialized in the distribution to the offspring of hereditary characteristics, while embryology concerned itself with the conversion of the egg into the adult. The former dealt with the events during the two cell-generations which comprise the maturation of the germ-cells and their fertilization, while the latter grappled with what happened during the fifty cell-generations which separate the fertilized egg from the full-grown man.

Now these two sciences are coming together again, for the factors concerned in hereditary resemblance are clearly also responsible for controlling development. After outlining the salient facts of embryology, Professor Waddington deals with the role of Mendelian genes in controlling development pathways, the activation of genes by the cytoplasm and their inhibition, and the synthesis of new substances. He is then able to formulate principles governing the differentiating system, the origin of pattern, and the production of shape. He has produced a most stimulating book which will be essential both to geneticists and embryologists.

G. DE BEER

ANTIMETABOLITES AND CANCER

Antimetabolites and Cancer, *edited by C. P. Rhoads. Pp. vi + 312. American Association for the Advancement of Science, Washington.* 1955. $5.75 *net.*

This collection of papers, although given at a Symposium in December 1953, constitutes a review of the field which is still, in most of the essentials, up to date. Admirable papers by Hitchings, Burchenal, Mandel, Lansford and Shive, Parks, and G. B. Brown deal with widely investigated aspects of the use of purine, pyrimidine, and folic acid analogues as antimetabolites and describe what is known of their relation to the treatment of experimental and clinical malignant disease.

In this connection, papers by Skipper, and by Nichol and Welch, on the development of resistance by A-methopterin and 8-azaguanine are particularly interesting. Woolley describes the inhibition of mouse-tumour growth by analogues of 1 : 2-diamino-4 : 5-dimethylbenzene (a vitamin B_{12} precursor), and among several interesting papers on the less well explored parts of the field may be mentioned investigations on plant growth and plant tumours by Nickell, of the effect of aminopterin on bone-marrow by Totter; on the use of nucleotide and nucleoside analogues as antimetabolites by Visser; and by Nelson on the effect of antimetabolites in the induction of foetal abnormalities. An interesting paper by Weinhouse on the carbohydrate metabolism of tumour cells brings this important but relatively neglected topic up to date.

This book can be highly recommended to those requiring a stimulating and authoritative account of much of the work done on those antimetabolites which have been investigated thoroughly.

G. M. TIMMIS

LUNG CANCER

Causal Factors in Cancer of the Lung, *by Carl V. Weller. Pp. viii + 113. Charles C. Thomas, Publisher, Springfield; Blackwell Scientific Publications Limited, Oxford.* 1956. 21*s.* 6*d. net.*

Dr Weller's book is on the theme of the day in cancer research—that cigarette smoking is the principal cause of the huge rise in the lung cancer rate in the last few decades. He presents, in not too technical a fashion, the evidence unravelled by the work of the Kennaways, Doll and Hill, Clemmesen, Dorn, Cutler and Loveland, Hammond and Horn, and others.

Dr Weller first uses the statistical material for his treatment of the subject and then discusses the appalling death rate from lung cancer among the miners at the Schneeberg and Joachimstal mines; there are some interesting illustrations of the miners from woodcuts dating back to 1556. He next reviews agents and conditions which have been implicated as carcinogens for the lung: arsenic, radioactivity, silicosis, asbestosis, pneumonitis, chromates, benzpyrene, atmospheric pollutants, urbanization, and tobacco.

However, when Dr Weller has assembled the impressive evidence, if not indeed proof, that cigarette smoking is responsible for something like 80 per cent of the present formidable toll of lung cancer deaths, he becomes extremely cautious on the question of prevention.

The best he can do is to shift the responsibility on to the shoulders of two cancer investigators made of somewhat bolder stuff, for he quotes Maisin and Clemmesen, who stated in 1952: 'May we show the same practical sense as our forefathers, and not look for direct proofs which are out of reach before we transmit experience into practical measures.' I. HIEGER

BRITISH PHARMACOPOEIA

British Pharmacopoeia 1953: Addendum 1955. *Pp. xvii* + 94. *The Pharmaceutical Press, London.* 1955. 21*s. net.*

The publication of an addendum two years after the last edition of the *British Pharmacopoeia* shows a great determination to keep up with the continuous succession of new medicaments. Perhaps the most generally interesting inclusion is that of Soluble Aspirin Tablets. There are several new monographs, which include important substances like cortisone and oxytetracycline.

The Pharmacopoeia Commission has gradually cast aside one after another the prejudices which formerly governed decisions on what a monograph might contain, with the result that now the *British Pharmacopoeia* has become a useful book for everyone except for the physician! We have, for example, in this addendum monographs on diethylcarbamazine citrate, iopanoic acid, phenindione, and others of which it is safe to say that not one physician in a thousand would know the use. Why cannot a clue be given? Some uses are already given, as for example, the dose of cortisone acetate. Cannot the Commission now take the plunge?

J. H. BURN

AMERICAN MEN OF SCIENCE

American Men of Science (*ninth edition*), *Vol. II* (The Biological Sciences). *Pp.* 1276. *The Science Press, Lancaster, Pa; Bowker Company, New York.* 1955. $20 *net.*

This is the second volume of the new edition of 'American Men of Science', and is devoted to those working in the fields of zoology, botany, medical research, and kindred fields. It includes some thirty thousand names, compared with nearly forty-four thousand in the recently published volume, which deals with physical sciences. Wherever practicable, workers in borderline fields such as biochemistry and biophysics have been offered the choice of appearing in either Volume I or Volume II, but to avoid confusion there are ample cross-references from one volume to the other.

This volume follows much the same style as that for the physical sciences: the only obvious difference between the two volumes—and one which seems as unnecessary as it is inconvenient—is that the page sizes differ so that they range untidily in the bookshelf. It is a mine of concise and comprehensive information, and will be indispensable as a work of reference to all interested in the organization of scientific work in the United States. The nature of the work requires that a general review shall be brief, but brevity is here in no way indicative of lack of appreciation. The preparation of such a work is obviously a heavy undertaking, and one must be grateful to those whose combined efforts brought it to so satisfactory a conclusion.

A third volume on similar lines will cover the social sciences.

TREVOR I. WILLIAMS

SCIENTIFIC BIOGRAPHIES

Biographical Memoirs of Fellows of the Royal Society. *Vol. 1. Pp.* 263. *The Royal Society, London.* 1955. 30*s. net.*

This is the first of a new series of annual publications continuing the Obituary Notices of Fellows of the Royal Society. The change of title does not reflect any major departure from the style of the former series, but it is none the less felicitous, for the phrase 'obituary notice' suggests a bleakness which these volumes do not deserve. They tell stories of outstanding contributions to science: this is inevitable from the nature of the volume. But they do much more than this: many of them tell moving stories of men who were in no sense narrow specialists but lived full and active lives with a wealth of interests. Were it worth while to refute the criticism, still sometimes heard, that scientists are unemotional materialists, abundant evidence could be found here. This series of volumes can be an inspiration to the present generation; to those of the future they will prove also a unique source of authentic biographical information.

TREVOR I. WILLIAMS

LUDWIG BOLTZMANN

Ludwig Boltzmann, *by Engelbert Broda. Pp. viii* + 152. *Franz Deuticke, Vienna.* 1955. *Paper covers, DM* 9.50 *net; linen, DM* 11 *net.*

Ludwig Boltzmann was the last of the great theoretical physicists of what is now called the classical epoch. In 1906, at the age of sixty-two, he died by his own hand. Planck's first exposition of the quantum theory had, it is true, appeared in 1900 and Einstein's first paper on relativity in 1905, but Boltzmann's best work was over by the turn of the century. He had before then made his fundamental advances in the kinetic theory of gases, at a time when the atomic theory was far from being generally accepted. In particular, he had systematically developed the conception of probability as an essential part of gas theory and he had done his pioneering work as a founder of statistical physics.

Boltzmann was a most interesting character. He was a lecturer who, by his character and clarity, attracted enthusiastic audiences; he was a deep thinker in philosophical matters; he had a keen and dry sense of humour. All these aspects of the man are developed in a most interesting and understanding way in the little book before us, the first, we believe, to be devoted to him. It is divided into three sections—The Man: The Physicist: The Philosopher. The first is particularly valuable because the author has had personal communications from many, including Lise Meitner and Boltzmann's daughter and stepdaughter, who when they were young associated with the great man. Their recollections contribute to a particularly personal and animated picture of one of the pioneers of science.

E. N. DA C. ANDRADE

Some books received

(*Note.* Mention of a book on this page does not preclude subsequent review.)

ASTRONOMY

Introduction to Astronomy, *by Cecilia Payne-Gaposchkin. Pp.* x + 508. *Eyre and Spottiswoode, London.* 1956. 50*s. net.*

The Planet Venus, *by Patrick Moore. Pp.* 132. *Faber and Faber Limited, London.* 1956. 15*s. net.*

BIOCHEMISTRY

Essays in Biochemistry, *edited by Samuel Graff. Pp.* x + 345. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1956. 52*s. net.*

BIOGRAPHY

Robert Hooke, *by Margaret 'Espinasse. Pp. vii* + 192. *William Heinemann Limited, London.* 1956. 21*s. net.*

BIOLOGY

Einführung in die Mikropaläontologie, *by Horst Werner Matthes. Pp. viii* + 348. *S. Hirzel Verlag, Leipzig.* 1956. *DM.* 33.40.

Hormones Hypophysaires Somatotrope et Corticotrope. Croissance et Métabolisme, *by H. Tuchmann-Duplessis. Pp.* 319. *Masson et Cie., Paris.* 1956. *Fcs* 2200.

Proceedings of the Underwater Physiology Symposium, *edited by Loyal G. Goff. Pp. xi* + 153. *National Academy of Sciences—National Research Council, Washington.* 1955. *Paper bound,* $1.50.

La Régulation des Processus Métaboliques dans l'Organisme, *by Théophile Cahn. Pp. xii* + 681. *Presses Universitaires de France, Paris.* 1956. *Fcs* 3000.

BOTANY

A Book of Wild Flowers. 160 *Plates after Watercolours by Elsa Felsko. Notes by Sheila Littleboy. Pp. xi* + 231. *Bruno Cassirer, Oxford; Faber and Faber Limited, London.* 1956. 35*s. net.*

CHEMISTRY

The Determination of Toxic Substances in Air, *edited by N. Strafford, C. R. N. Strouts, and W. V. Stubbings. Pp. xxvii* + 226. *W. Heffer and Sons Limited, Cambridge.* 1956. 35*s. net.*

Geochemistry of Iodine. Bibliography 1825–1954. *Pp. viii* + 150. *Chilean Iodine Educational Bureau, London.* 1956.

Introductory Quantitative Chemistry, *by A. R. Olson, C. W. Koch, and G. C. Pimentel. Pp.* x + 470. *W. H. Freeman and Company, San Francisco; Bailey Bros. and Swinfen Limited, London.* 1956. 42*s.* 6*d. net.*

Modern Chemical Processes, *Vol.* IV, *by the Editors of* Industrial and Engineering Chemistry. *Pp. v* + 202. *Reinhold Publishing Corporation, New York; Chapman and Hall Limited, London.* 1956. 40*s. net.*

The Petroleum Acids and Bases, *by H. L. Lochte and E. R. Littmann. Pp.* 368. *Constable and Company Limited, London.* 1956. 50*s. net.*

Physikalisch-chemisches Rechnen in Wissenschaft und Technik, *by Hans Fromherz. Pp. ix* + 316. *Verlag Chemie G.m.b.H., Weinheim/Bergstr.* 1956. *DM.* 32.50.

CRYSTALLOGRAPHY

Echt oder synthetisch? *by K. F. Chudoba and E. J. Gubelin. Pp.* 156. *Rühle-Diebener-Verlag K.G., Stuttgart.* 1956. *DM.* 18.50.

ENGINEERING

Automatic Process Control for Chemical Engineers, *by N. H. Ceaglske. Pp. xiv* + 228. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1956. 54*s. net.*

Dizionario d'Ingegneria, *Vol. V,* RUM–Z, *edited by Eligio Perucca. Pp. xii* + 1046. *Unione Tipografico—Editrice Torinese, Turin.* 1956. *Lire* 12 000.

Fluidization, *edited by D. F. Othmer. Pp. ix* + 231. *Reinhold Publishing Corporation, New York; Chapman and Hall Limited, London.* 1956. 56*s. net.*

Frequency Response, *edited by R. Oldenburger. Pp. xii* + 372. *The Macmillan Company, New York.* 1956. 52*s.* 6*d. net.*

Ingegneria Nucleare, *by F. Mazzoleni. Pp. xii* + 470. *Ulrico Hoepli, Milan.* 1956. *Lire* 4000.

MATHEMATICS

Automatic Digital Computers, *by M. V. Wilkes. Pp.* x + 305. *Methuen and Company Limited, London.* 1956. 42*s. net.*

The Theory of Games and Linear Programming, *by S. Vajda. Pp.* 106. *Methuen and Company Limited, London; John Wiley and Sons Inc., New York.* 1956. 8*s.* 6*d. net.*

MEDICINE

Ciba Foundation Colloquia on Endocrinology, Volume IX. Internal Secretions of the Pancreas, *edited by G. E. W. Wolstenholme and C. M. O'Connor. Pp. xii* + 292. *J. and A. Churchill Limited, London.* 1956. 40*s. net.*

Histamine (Ciba Foundation Symposium in honour of Sir Henry Dale), *edited by G. E. W. Wolstenholme and C. M. O'Connor. Pp. xvi* + 472. *J. and A. Churchill Limited, London.* 1956. 50*s. net.*

Les Mécanismes Cérébraux de la Prise de Conscience, *by P. Chauchard. Pp.* 240. *Masson et Cie., Paris.* 1956. *Fcs* 1300.

Psychopharmacology, *edited by N. S. Kline. Pp.* x + 165. *Publication No.* 42 *of the American Association for the Advancement of Science, Washington; Bailey Bros. and Swinfen Limited, London.* 1956. 32*s. net.*

PHYSICS

The Mathematics of Diffusion, *by J. Crank. Pp. vi* + 347. *Clarendon Press, Oxford.* 1956. 50*s. net.*

Measurement of Small Holes, *by I. A. Grigor'ev.* (*Translated from the Russian by the Department of Scientific and Industrial Research.*) *Pp.* x + 137. *Her Majesty's Stationery Office, London.* 1956. 8*s.* 6*d. net.*

Temperature. Its Measurement and Control in Science and Industry, *Vol.* II, *edited by H. C. Wolfe. Pp.* x + 467. *Reinhold Publishing Corporation, New York; Chapman and Hall Limited, London.* 1955. 96*s. net.*

TECHNOLOGY

Atom Harvest, *by L. Bertin. Pp.* 253. *Secker and Warburg, London.* 1955. 20*s. net.*

Glass, *by G. O. Jones. Pp. vi* + 119. *Methuen and Company Limited, London; John Wiley and Sons Inc., New York.* 1956. 8*s.* 6*d. net.*

High Temperature Technology, *edited by I. E. Campbell. Pp. xiv* + 526. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1956. 120*s. net.*

Plastics in the Service of Man, *by E. G. Couzens and V. E. Yarsley. Pp.* 315. *Penguin Books, Harmondsworth, Middlesex.* 1956. 3*s.* 6*d. net.*

Notes on contributors

H. E. HUXLEY,
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Was born in 1924 and was educated at Park High School, Birkenhead, and at Christ's College, Cambridge. During the war served as a radar officer in the Royal Air Force, working also at the Telecommunications Research Establishment, Malvern. Research student in the Medical Research Council Unit, Cavendish Laboratory, Cambridge (1948–52), where he was awarded a Ph.D. for a thesis on X-ray diffraction studies of muscle. Subsequently spent two years in the United States as a Commonwealth Fund Fellow, where he continued working on muscle and developed a strong interest in electron microscopy. On his return to the Medical Research Council Unit in Cambridge he became a Fellow of Christ's College. Now an External Staff Member of the Medical Research Council, and Research Associate in the Department of Biophysics, University College, London, where his main interests lie in the study of the molecular structure of biological systems by means of electron microscopy and other techniques.

SIR EDWARD BULLARD,
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Was born in 1907 and educated at Repton School and Clare College, Cambridge. He began research under Lord Rutherford in 1929, working on the scattering of slow electrons in gases. In 1931 he took up geophysics and has done experimental work on gravity, seismology, and the measurement of heat flow on land and at sea. From 1950 to 1955 he was Director of the National Physical Laboratory, and is now Assistant Director of Research in Geophysics in the University of Cambridge. He has written extensively on the origin of the earth's magnetic field and on magneto-hydrodynamics.

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Was born in 1901 and was educated at Ealing County School; Birkbeck College, University of London; and Trinity College, Cambridge. From 1932 to 1953 he was Professor of Mathematics at Kings College, University of London, but during the war years was seconded to the Royal Aircraft Establishment, Farnborough. Is now Sedleian Professor of Natural Philosophy, University of Oxford, and Fellow of The Queen's College, Oxford. He is the author of several works on quantum theory and other branches of mathematical physics.

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Was born in 1914 and was educated at Durham Grammar School and the University of London. During the war he served in the Ministry of Supply, working in the Royal Society Mond Laboratory, Cambridge, and is now a lecturer at University College, London. His research work has been concerned with the physical properties of liquids in the normal, supercooled and superheated states. In 1955 a grant from the Astor Foundation enabled him to work on bubble chambers at the University of Michigan and to study the various developments of these new detectors in other parts of the United States.

T. M. HARRIS,
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Born at Leicester, 1903. Was trained in fossil botany by H. S. Holden at Nottingham and by A. C. Seward at Cambridge. Appointed Professor of Botany at Reading University in 1934. Member of Danish geological expedition to East Greenland 1926–7. Has written numerous papers on fossil plants from Greenland and later from the Yorkshire coast.

R. D. KEYNES,
M.A., Ph.D.,

Born in London, 1919; educated at Oundle School and Trinity College, Cambridge. Fellow of Trinity, 1948–52. Fellow of Peterhouse since 1952, and University Lecturer in Physiology since 1953. From 1940 to 1945 worked for the Admiralty on Asdics and naval radar. Since 1946 his main field of research has been the use of radioactive isotopes to investigate the ionic interchanges of nerve and muscle fibres. In 1951 he spent three months at the Instituto de Biofísica, University of Brazil, Rio de Janeiro, as Visiting Reader in Biophysics.

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